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Modeling and Simulation

Tools for Management of Veterinary Pests

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ARS-46

Modeling and Simulation

Tools for Management of Veterinary Pests

Edited by
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Agricultural Research Service
U.S. Department of Agriculture

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PREFACE

This publication results from a symposium on "Modeling and Simulation: Tools for Management of Veterinary and Medical Pests." The symposium, sponsored by USDA-ARS, USDA-CSRS, and SAES, was held in conjunction with the 28th Annual Livestock Insects Work Conference, July 9-12, 1984, Purdue University, West Lafayette, Indiana. Although papers dealing with medical pests were presented at the symposium, these were not submitted for publication here. Therefore, the title of this publication was changed to more accurately reflect its content.

The objectives of the symposium were: (1) to discuss approaches and problems in modeling pest populations important to livestock and medical entomology; (2) to promote the application of modeling and simulation to development of pest management strategies; and (3) to define future needs for information in modeling pest management systems.

This resultant publication is intended to provide a general background and starting point for research and extension efforts to use modeling and simulation as a tool in development of livestock pest management programs.

The efforts of the many people involved in organizing the meeting and preparing the manuscripts are greatly appreciated. As chairman of the steering committee, I want to thank the members of the committee, I. L. Berry, ARS, Lincoln, NE; R. O. Moon, Univ. of Minnesota, St. Paul, MN; C. D. Steelman, Arkansas Ag. Experiment Station, Fayetteville, AR; D. E. Weidhaas, ARS, Gainesville, FL; and S. M. Welch, Kansas State Univ., Manhattan, KS, for their work in organizing and implementing the symposium. We, the steering committee, wish to thank R. A. Bram, NPS-ARS, Beltsville, MD, for proposing the project and encouraging our efforts in carrying out its objectives. We also thank R. E. Williams, Purdue Univ., for his invaluable assistance in local arrangements. Each paper contained in this volume was independently reviewed and refereed by knowledgeable scientists in the subject area. We appreciate the contribution of both the authors and the reviewers. Finally, we thank Kay McDonald, ARS Information Office, for her guidance in preparation of the publication.

J. Allen Miller, Chairman
Steering Committee

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MODELING AND SIMULATION: TOOLS FOR MANAGEMENT OF VETERINARY AND MEDICAL PESTS

INTRODUCTION

R.A. Bram[1/]

Modeling and simulation are not new to veterinary and medical entomology. Entomologists, statisticians, agricultural engineers, and other scientists have long been incorporating modeling and simulation concepts when devising strategies to control or manage disease vectors and arthropod pests of man and animals. A classic, early example could be cited from the development of the screwworm eradication program by use of the sterile insect technique. Knipling[2/], with pad and pencil, addressed such important questions as: what level of sterility must be achieved for eradication?; how many sterile flies must be released?; how often must sterile fly releases be made?; what is the optimum distance separating release lanes?; and many other parameters. Innumerable other examples of successful early applications of modeling and simulation concepts exist. However, today technology has advanced to the point where scientists may become infinitely more sophisticated in the application of modeling and simulation concepts. Because of the computer revolution, the capability now exists for storing, retrieving, manipulating, and displaying a biological data base that was inconceivable just 10 years ago.

Now, a critical mass of medical and veterinary entomologists and other scientists are utilizing modeling and simulation as tools for research to manage, control, and even eradicate arthropod pests and disease vectors that affect man and animals. Although the stated purposes of this Workshop were to discuss approaches and problems in modeling arthropods of medical and veterinary importance, to promote the application of modeling and simulation for development of pest management strategies, and to define future needs for information, the Workshop also fulfilled other unstated purposes. The value of informal interactions between individuals working on solutions to related problems through the use of modeling and simulation as tools, or the educational opportunity for those scientists who have never considered modeling or simulation as tools in their research approaches, should not be underestimated. The fact that 80 scientists participated in the opening session of this Workshop reflects the current high level of need for and interest in this subject. By assembling at this Workhop, a benchmark can be established of where we are today, and this awareness will point the way to our future direction.

What of the future? I suggest that research as well as large-scale pest management programs, whether domestic or international, will depend more and more on model systems and computer simulations. In the Secretary of Agriculture's 1984 report to the Congress on needs assessment for the food and agricultural sciences he states[3/]: "Model systems and computer simulations are being developed specifically for agricultural research, and more are needed" (my italics). He further states that: "Training is needed to encourage computer literacy among professionals and among adult and youth clientele." When models are accurately developed and verified, they can be effective tools for research as well as for solving real-time problems on the farm or throughout entire counties, states, or countries. I am not proposing that this Workshop will lead medical and veterinary entomologists and other scientists to conduct research on Expert Systems--yet. But the future is open ended. When fully developed and verified, models and simulations for the control of arthropods of medical and veterinary importance will at first stand on their own as research tools or be modified for inclusion in an extension system such as AGNET or BUGNET. They may be no more than subroutines of a single model for managing the entire farm operation. Eventually, Expert Systems will be developed for agriculture and it is my opinion that these systems must include a component to address those insects, ticks, and mites that affect man and animals.

I wish to commend the 1983 U.S. Livestock Insects Workshop for its foresight in endorsing this Workshop and the State agricultural experiment stations, the USDA Cooperative State Research Service, and the USDA Agricultural Research Service for serving as the Workshop sponsors. The Steering Committee did a magnificent job of developing an outstanding program that provided for discussions of broad topics which are applicable to a variety of modeling, simulation, and validation efforts, for reports on existing models, and for even an opportunity to actually demonstrate working models.

Publication of these proceedings is a good beginning to document the current state of our knowledge and, I would hope that the Workshop, itself, has fostered a continuing dialogue between scientists applying the concepts of modeling and simulation to the control of those

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2/ Knipling, E. F. 1955. Possibilities of insect control or eradication through the use of sexually sterile males. J. Econ. Ent. 48:450-462.

3/ Block, J. R. 1984. Summary: Needs assessment for the food and agricultural sciences. A report to the Congress from the Secretary of Agriculture: 55-56. Joint Council on Food and Agricultural Sciences, Washington, D.C.

arthropods that affect animals and man. Perhaps, in 3-5 years another Workshop will be held in which a quantum leap in the state of our knowledge and capabilities will be recognized. I challenge you to provide at least one model system or computer simulation for each of the major arthropods affecting man and animals at the next Workshop.

PROCESS MODELING, SIMULATION AND VALIDATION FOR POIKILOTHERMS

Guy L. Curry[1] and Richard M. Feldman[2]

INTRODUCTION

Systems analysis involves the activities of description, explanation, and control of a system's behavior over time. In general, a system refers to any collection of components along with the relationships between these components. In a modeling context, it is often convenient to make a distinction between the system and its environment. All components described or modeled are included as part of the system. The environment consists of those factors that drive the system (modeled components) but are not themselves modeled. Instead, the environmental factors must usually be monitored. Thus, the system behavior is guided or influenced by its environment. For example, a typical population process treats the insects and host plants as system components, and temperature as an environmental factor. The modeling effort is directed at describing the insect/plant dynamics, treating temperature and other factors as "driving forces". As another example, consider a field population of insects. The population growth of insects, which may be the system aspect that we are modeling, is certainly influenced by immigrating and emigrating populations. Thus, when a global context is of interest, the system includes the in-field, immigrating, and emigrating components. When focusing on a single field, however, we may choose to measure the immigrating and emigrating populations instead of modeling them, and thus these migrating populations would be considered as environmental components instead of system components.

The descriptive aspect of systems analysis (i.e., model development) is the critical activity in the analytical procedure. Because we wish to use the model to explain and/or control the behavior of the biological system, the degree of reality contained in the model is of paramount importance. Rarely will quality analyses result from subquality models.

SYSTEM MODELING

It should be realized that a model is merely an abstraction of the real system. Hence, every model has its limitations and validity range. The level of detail or descriptive depth needed in a model depends on its intended use. For example, plane geometry is a collection of geometrical relationships that have great utility and mathematical validity within the context of their environment. However, a basic assumption like "parallel lines never intersect" is not adequate in the context of global travel, where spherical geometry must be applied. Thus plane geometry may be suitable to describe short-range travel, but the additional complexity of spherical geometry is needed to describe long-distance travel. Similarly, in modeling biological systems, "trade-off" decisions must constantly be made where realism conflicts with tractability.

The selection of the system boundaries, the segmentation of the environment and the system into components, and the descriptive modeling of the system components involve both science and art. Once the system has been defined and the segmentation of the components made, the system modeling can commence. Modeling the population dynamics of poikilotherm organisms can be categorized into three general phases: (1) the description of the system, (2) the description of individual components, and (3) the synthesis of the components into an integrated model. The monograph by Curry and Feldman (1986) deals in detail with each of these phases.

As with the analysis of any problem, the physical and biological domain of concern should first be decided, including both the time aspect and the physical region of interest. This domain determines the approach for analysis, the components of the system that must be considered, and possibly the applicable level of detail.

If we are attempting to model a statewide pest population, for example, then migration across the system boundaries (state borders, in this instance) may not be of concern. If our goal is to model a particular field, on the other hand, migration across the system boundaries probably should be considered, since many pest populations are significantly influenced by migration.

A similar analysis is applicable for the time aspect and its impact on the general level and detail needed for modeling purposes. If long-term studies are of interest for a pest population, then the overwintering survival fractions must be included in the population model, since they are major driving forces in long-term behavior. However, if pest control during a single growing season is the focus, then the overwintering insects do not necessarily need to be part of the system; they could be treated instead as an environmental component that is measured (sampled) at the start of the season and then used to initiate the model. From this initiation, it may be possible to adequately model the population dynamics of a field throughout the critical decision period for crop yields.

The modeling technique selected for a biological system can be one of a variety of general classes. Two major considerations are whether to take a deterministic or a stochastic approach, and whether to utilize discrete or continuous states. In deterministic models, we attempt to predict or model the mean value of the process without explicitly considering statistical variations; a stochastic approach includes probabilistic aspects of the system. The choice of states means treat-

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ing the system parameters as either discrete (as in integers) or continuous variables. Although mixtures of these can be accomplished, most population models are of the deterministic continuous variety.

Some population and component models utilize stochastic concepts in arriving at mean-value estimators. For example, one approach to estimating insect emergence from the immature to the adult phase uses a probability distribution describing the duration of the immature phase on a suitable biological age scale (Curry et al. 1978a). This approach takes into account the probabilistic aspects of emergence, but its goal is to improve the mean-value prediction of emergence times. In general, a stochastic model is more realistic and facilitates a proper statistical validation analysis, but the computation of variances for population models is at present a greatly needed but much underdeveloped research area (Feldman et al. 1984).

Even though biological organisms are in fact discrete elements, the large numbers involved generally favor a continuous modeling approach. The use of fractional numbers within a model will have little detrimental effect on the model predictions if the base number is large. If the population numbers are very small, however, the population sample path would not be well approximated by the use of fractional numbers.

Another general concern is the mathematical representation of the model and the associated numerical implementation in a computer algorithm. It is often convenient to represent population models as differential or partial differential equations (Von Foerster 1959). From a computational point of view, a discrete approximation of the state space (biological time and population numbers) must be employed to obtain the population's time-dependent behavior numerically. Discrete approximations are made in several ways. Standard finite difference numerical analysis can be used with the differential equations that describe the system, or the population can be represented by a matrix model which is a discrete analogue to the continuous differential equations. Another procedure is cohort modeling (Curry et al. 1978b), which groups organisms according to biologically meaningful classes. This approach facilitates individual component validation, since the groupings (cohorts) are those commonly used in individual process studies. Conceptually, these various methods yield the same numerical results, given equivalent state-space increments.

VALIDATION-CALIBRATION

Model validation implies that the model accurately describes the entire physical system and the system's responses to the environment. In a strict sense, total model validation is never possible, since a model by definition is an abstraction of a real-world process. However, we use the term validation to mean that the model captures the pertinent behavior of the real system. Computer models are often validated in another sense in that they are certified as an accurate translation of the mathematical model into a computer program. This type of validation, called verification, merely establishes that the computer code is functioning properly; it does not validate the proper behavior of the model.

One approach for validating a mean-value model is to formulate a statistical hypothesis that the model's predicted values equal the true mean values for the system under observation. Even when this approach can be properly applied, there is no absolute guarantee that the model is valid. Statistical tests are devised so as to have a high (known) probability of rejecting a false hypothesis and a relatively low probability of rejecting a valid hypothesis. When a statistical hypothesis is rejected, there is a known (usually denoted by α) probability of making an error. When a statistical hypothesis is not rejected, the probability of making an error is usually unknown, with a maximum possible value of $1 - \alpha$. Unfortunately, even though the error bounds seem large for statistically accepting the hypothesis that the model is predicting accurately, statistical tests are the best available objective method for model validation.

If population numbers over time are modeled, then several independent populations must be sampled throughout the period of concern in order to perform a statistical validation. Under field conditions, it is expensive to sample intensively even a single population through time; to monitor several independent populations is even more difficult and costly. However, the major difficulty for biological systems is to obtain different populations that have identical conditions. Repeated sampling from a single population reduces the sampling error associated with assessing that specific population value but does not estimate the inherent biological variation.

One validation procedure often used is to establish confidence intervals associated with the measurement error for sample means through time for a given population; model predictions are then compared to the sampling results. The tendency is to say that the model is valid if the predictions fall within the error range for each sample point, but it is easy to see that this is an improper procedure by considering its logical outcome; it could lead to the erroneous conclusion that bad sampling methods (larger sampling error range) produce a better model, since the model would be "validated" more frequently with larger sampling error ranges. On the other hand, if sampling were performed without error, the model would almost never be" valid", since it is unlikely that the model would predict each sample mean exactly through time.

The underlying problem of validation is determining whether the model reproduces the growth or decline that is reasonably likely for the actual population. Under identical conditions the population could take many trajectories of which we generally have sampled just one. If we knew the distribution of these trajectories, then we could perform a statistical comparison to validate

the model. To obtain an estimate of the distribution of the population trajectories, we need to sample several independent populations under identical conditions, or we need a model that predicts variances and covariances as well as mean values. Unfortunately, very few models predict other than mean trajectories. We are not aware of methods for population modeling with enough realistic structure to be of practical use in pest management that include predictions of variances.

In summary, testing of the model behavior is usually done with insufficient data to properly assess the model's validity as a surrogate for the true population. Often, models validated for a given location fail miserably in other geographical regions, although an adjustment of some of the parameter values will frequently result in acceptable model behavior for the new region. This parameter-setting procedure for each general region is called model calibration.

It is not surprising that even a "good" model must be recalibrated for different situations. In general, models lack the structure to set parameters automatically; to extend a model to cover these missing aspects may not even be possible with the current knowledge base. In general, there is a trade-off between the utility of a more detailed model and the expense of further refinement. Therefore, model calibration to adjust the model to various site conditions should be an accepted and routine procedure.

MODEL UTILIZATION

The depth of development of a model is dependent on its envisioned use. Models that are to be used to guide research, such as indicating to plant breeders the sensitivity of an insect pest to changes in various plant characteristics, must be very detailed in the plant/insect interaction components. If spraying decision analyses are to be performed, a crop model that will respond accurately to pest damage is needed. In this latter case, the model need not be of a level which can predict the yield for a given field; but more importantly, the yield level must be controllable and be responsive to pest population levels. Thus, the purpose of the model should be clearly defined at the onset of the model development phase.

The wide spread availability of personal computers has added a new dimension to the possible utilization of biological models. Complex computer models which five years ago were restricted to large mainframe computers are running with surprising efficiency on 16 bit computers of the IBM-PC class. As an illustration, a cotton crop model that has approximately a two-minute execution time on an IBM mainframe will execute on an IBM-compatible micro using a floating point coprocessor in the same approximate length of time. Thus, models not previously available to producers can in the near future be used to help make day-to-day operational decisions in the producer's office.

COMPONENTS

Our approach to modeling population dynamics is to separate the general process into its component parts: developmental timing, reproduction, innate mortality, external mortality, and movement. Individual components can generally be measured and analyzed more easily in isolation; however, the experiments set up to isolate the specific component often induce an artificial aspect into the measurements. The resultant component model will therefore have to be recalibrated, using data from general population studies.

The temperature description of poikilotherm responses for all components warrants discussion. The characteristics of these responses are usually consistent but difficult to discern under naturally varying environmental regimes. The concept of a temperature-dependent rate function has been utilized with considerable success since the late 1800s. One particularly useful specialization of this concept is the degree-day procedure. Roughly speaking, the degree-day rule allows a chronological to biological time transformation that alleviates most of the temperature dependency. The common procedure is to associate a fixed number of degree-day units with the completion of the process; however, a more accurate method is to utilize a distribution of completion times on the degree-day scale. This latter approach results in the completion times being distributed for a group of individuals, which is a commonly observed phenomenon.

Individual components are analyzed and modeled on the basis of the environmental factors affecting their behavior. The component models are validated/calibrated individually; then the components are integrated into a general population model. This synthesis process requires both individual component validation checks and composite response verification. As previously stated, the individual components may need to be recalibrated utilizing the population response data. Methods of organizing the components into an aggregate model include the Von Foerster (1959) partial differential equation structure and the stochastic cohort model of Curry *et al.* (1978b).

CONCLUSIONS

Reasonably complete models for pest management purposes include the papers by Haynes and Tummala (1976), Holling *et al.* (1976), Jones (1976), Wang *et al.* (1977), Curry *et al.* (1980), Ruesink *et al.* (1980), and Feldman *et al.* (1981). These works illustrate the component nature of large models and their synthesis into a full systems models. Getz and Gutierrez (1982) and Feldman and Curry (1982) review systems analysis for crop protection and pest management and the Conway (1984) book covers several models and analyses for pest and pathogen control. The optimization of these complex models with respect to control parameters is generally best accomplished by using heuristic search procedures. Mathematical search procedures such as those based on conjugate transformations are extreme resource users; for example, they may

require the model to be completely rerun more than 100-200 times for each analysis (Talpaz et al., 1978; Gutierrez et al., 1979). An extremely efficient algorithm utilizes the dynamic programming approach (Shoemaker 1973, 1982), but this procedure's severe restrictions concerning the biological interactions limit its general applicability. Two general areas in which research is greatly needed are the modeling of statistical population properties and the development of efficient optimization algorithms for pest control policies. The book by Curry and Feldman (1986) discusses all of these modeling aspects in detail.

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MANAGING INSECTICIDE RESISTANCE: INSIGHTS THROUGH SIMULATION

Bruce E. Tabashnik[1]/ and Brian A. Croft[2]/

INTRODUCTION

Resistance to insecticides in insect and mite pests poses a serious threat to crop and livestock production, and to human health. Resistant strains of more than 400 arthropod species were recorded by 1980, including 168 insects and mites of medical or veterinary importance (Georghiou and Mellon 1983). Unfortunately, pests have developed resistance faster than beneficial arthropods, limiting the integration of biological and chemical control (Croft and Strickler 1983). The goals of resistance management are to retard resistance development in pests, and to promote it in beneficials. We have used computer simulation as a tool for working towards these goals (Tabashnik and Croft 1982, 1985). In the present paper, we (1) review research on a general model of insecticide resistance, (2) describe attempts to validate models of insecticide resistance, and (3) suggest how insights from modeling might be applied to resistance problems with the horn fly (Haematobia irritans L., Diptera: Muscidae).

Management of insecticide resistance must be based on a fundamental understanding of resistance as an evolutionary phenomenon (Georghiou and Taylor 1976). Evolution of resistance is caused by increases in the proportion of individuals in a population which carry genes conferring resistance. Our use of models as a tool for devising resistance management strategies (fig. 1) began with a general model of resistance evolution (Tabashnik and Croft 1982). Next, we constructed and tested species-specific models of resistance evolution for 24 apple pests and natural enemies (beneficial predators and parasites) (Tabashnik and Croft 1985). Current research includes experimental validation of species-specific models and development of models which incorporate predator-prey interactions as well as resistance evolution (Tabashnik 1985).

Modeling Assumptions

Some key assumptions of our models (Tabashnik and Croft 1982, 1985) are (a) Resistance is controlled primarily by a single gene locus with two alleles, R (resistant) and S (susceptible), with a fixed dose-mortality line for each genotype; (b) the dose-mortality line for RS heterozygotes is intermediate between the SS (susceptible) and RR (resistant) lines. Thus, at low pesticide doses RS heterozygotes are not killed and the R gene is functionally dominant; at high doses, RS heterozygotes are killed and the R gene is functionally recessive (Curtis et al. 1978); (c) the insect life cycle is divided into 20 substages, with transition probabilities between substages determined by natural and pesticide mortalities; (d) immigrants are primarily susceptible and have at least one day to mate and reproduce before being subjected to pesticide mortality.

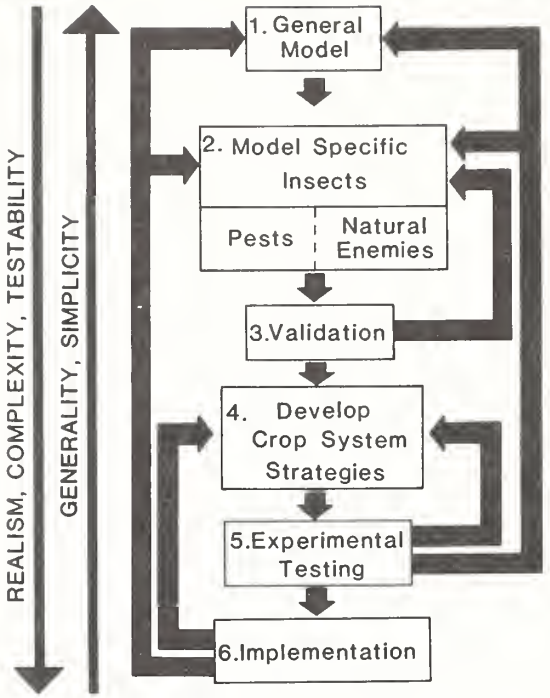

Figure 1. Using models to develop resistance management strategies.

RESULTS

General Model of Resistance Evolution

In the first phase of our study (Tabashnik and Croft 1982), we used a general model to examine the influence of various factors on rates of resistance development under four main classes of conditions (1) no immigration, low pesticide dose (R gene functionally dominant); (2) no immigration, high pesticide dose (R gene functionally co-dominant or recessive); (3) high immigration, low dose; and (4) high immigration, high dose. The four classes were chosen on the basis of previous work demonstrating the importance of immigration and functional dominance (Comins 1977, Curtis et. al 1978, Taylor and Georghiou 1979). Our results show that the way in which certain factors influence the rate of resistance evolution depends on which of the four classes of conditions are present. In other words, there are interactions among factors such that the same factor may have a different influence under different ecological and management conditions.

One of the most striking examples of the "interaction effect" is the influence of pesticide dose on the time to develop resistance (fig. 2).

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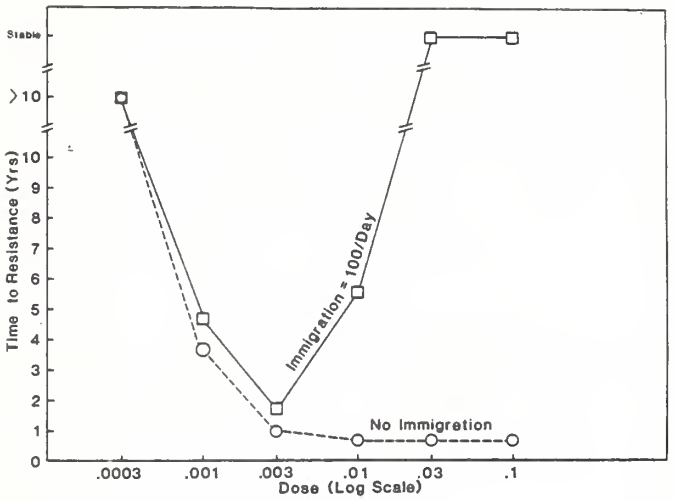
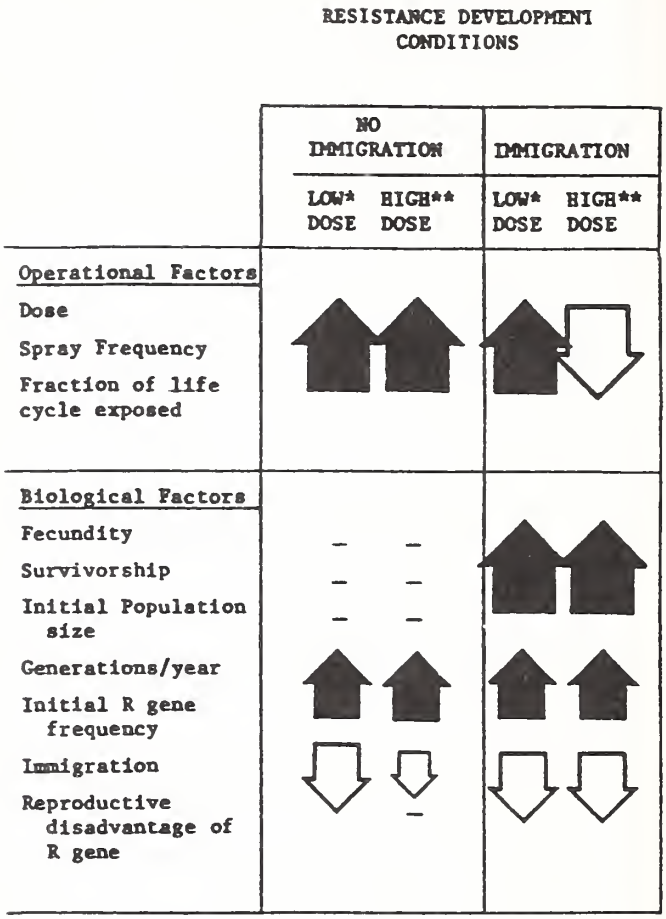


Figure 2. Effects of dose on the rate of evolution of resistance. Conditions: 0 or 100 immigrants daily, biweekly treatments of adults, two generations per year, time to resistance = time for population to reach the point after which the R gene frequency remains above 0.10 (after Tabashnik and Croft 1982).

Without immigration, resistance developed faster as dose increased. In contrast, with immmigration, there were two distinct phases. At low doses, resistance developed faster as dose increased, paralleling the case without immigration. At high doses, however, resistance developed more slowly as dose increased. These results are consistent with previous work (Comins 1977, Taylor and Georghiou 1979) and can be explained as follows: Without immigration, the rate of resistance development is determined primarily by the rate at which S genes are removed from the population. As dose increases, S genes are removed more rapidly, so resistance develops faster. The situation with low doses and immigration is similar. With immigration and doses high enough to kill RS heterozygotes, however, pesticide mortality also removes R genes from the population. As dose increases in this range, more RS heterozygotes are killed, leaving relatively few resistant (RR) individuals. RR survivors are effectively "swamped out" by susceptible immmigrants, thereby retarding resistance development.

We found that in the simulation, one of the most important factors influencing the rate of resistance evolution was the number of generations per year. Under all four classes of conditions, resistance developed faster as the number of generations per year increased. Field observations of resistance development in soil and apple arthropods (Georghiou 1980, Tabashnik and Croft 1985) are consistent with this pattern.

A summary of the influence of various factors on resistance development (fig. 3) highlights the interactions among factors. Increases in the



***Kills only SS, R gene functionally dominant**
****Kills SS and RS; or SS, RS, and some RR, R gene functionally co-dominant or recessive**

Figure 3. The influence of operational and biological factors on resistance development under 4 main classes of conditions. Black arrows pointing up show that increasing the listed factor speeds resistance development. White arrows pointing down show that increasing the listed factor slows resistance development. Dashes show little or no effect.

operational factors (dose, spray frequency, and fraction of the life cycle exposed to pesticide) made resistance develop faster when there was no immigration (both low and high dose range) and when there was immigration and a low dose. As previously described in detail, the opposite trend occurred when there was immigration and a high dose. Some biological factors (fecundity, survival, and initial population size) had little effect in the absence of immigration, but increases in these factors made resistance evolve faster when there was immigration. A few biological factors (generations/year and immigration) had the same influence under all four classes of conditions.

The most important conclusion from this general modeling approach is that the influence of certain factors will depend on the presence or absence of

immigration by susceptibles and on the functional dominance of the R gene (i.e. dose). Therefore, it is necessary to develop resistance management strategies that are appropriate for specific ecological and operational contexts.

Validation

In the second phase of our study we tested the model by comparing simulated times to evolve resistance with historically observed times to evolve resistance for 24 species of apple arthropod pests and natural enemies (Tabashnik and Croft 1985).

Apple arthropods were selected because apple has a low economic threshold for direct damage from pests and it is sprayed intensively (Croft and Hoyt 1983). Several pests and natural enemies associated with apple have developed resistance to azinphosmethyl (an organophosphorus pesticide), yet this compound has remained a major pest control tool for almost three decades because key apple pests have not become resistant to it (Croft 1982). The long-term patterns of evolution of resistance to azinphosmethyl among the diverse insects and mites inhabiting apple orchards in North America constitute a unique data set which can be used to test hypotheses about resistance. We sought to test the hypothesis that variation in rates of resistance evolution among apple species can be explained by differences in population ecology. We also used our model to test hypotheses proposed to explain why natural enemies develop resistance more slowly than pests.

To represent 24 different apple arthropod species in the simulation, the following population ecology parameters were estimated independently for each species: generations/year, fecundity, immigration, natural (non-pesticide) mortality, initial overwintering population size, development rate, sex ratio, pesticide exposure in orchards, and percent of time spent in orchards by adults. Parameter values and historically observed times to evolve resistance for each species were based on a survey of 24 fruit entomologists (Croft 1982).

Operational and genetic factors were held constant for all 24 species. Thus, all species were subjected to the same simulated pesticide dose, spray schedule and pesticide half-life. This is a reasonable assumption because all species were present in the same habitat and were exposed to a similar treatment regime. Dose-mortality lines and initial R gene frequency were also assumed to be the same for all species because these parameters are virtually impossible to estimate for most species. Further, we wanted to see how much of the variation in rates of evolution of resistance could be explained by differences among species in population ecology, with all other factors constant.

The results for the 12 pest species show a significant rank correlation between predicted (simulated) and historically observed times to evolve resistance (fig. 4a). Although predicted

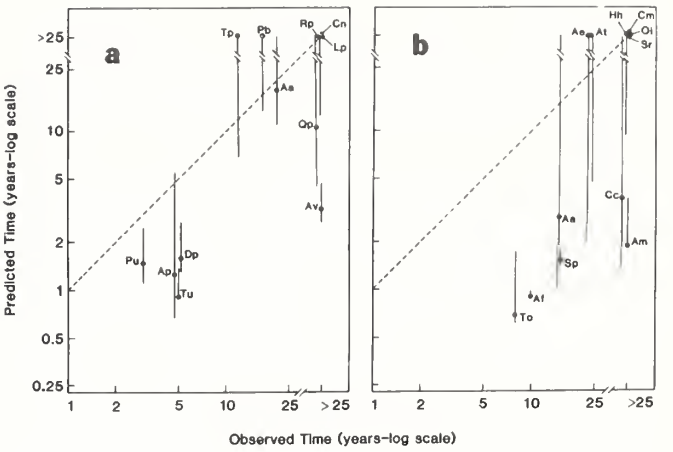


Figure 4. Predicted vs. observed times to evolve resistance to azinphosmethyl for apple arthropods. Predicted time (.) = simulated time to evolve resistance using means of estimates of population ecology parameters. Observed time = years after 1955 (first widespread use of azinphosmethyl) to first report of resistance. Vertical bars show range of predicted times from sensitivity analysis. Predicted = observed along the dashed lines. a. Pests. n = 12. Spearman's rank correlation coefficient, $r_s = .652$, $p < 0.05$. Aa = Archips argyrospilus, Ap = Aphis pomi, Av = Argyrotaenia velutinana, Cn = Conotrachelus nenuphar, Dp = Dysaphis plantaginea, Lp = Laspeyresia pomonella, Pb = Phyllonorcyter blancardella, Pu = Panonychus ulmi, Qp = Quadraspidiotus perniciousus, Rp = Rhagoletis pomonella, Tp = Typhlocyba pomaria, Tu = Tetranychus urticae. b. Natural enemies. n = 12. $r_s = .692$, $p < 0.025$. Aa = Aphidoletes aphidimyza, Ae = Anagrus epos, Af = Amblyseius fallacis, Am = Aphelinus mali, At = Aphelopus typhlocyba, Cc = Chrysopa carnea, Cm = Coleomegilla maculata lingi, Hh = Hyaliodes harti, Oi = Orius insidiosus, Sp = Stethorus punctum, Sr = Syrphus ribesii, To = Typhlodromus occidentalis. (after Tabashnik and Croft 1985).

times did not correspond perfectly with observed times, there was no consistent bias in the predictions (Kolmogorov-Smirnov two-sample test, $p>0.1$).

Recognizing the uncertainty in some population ecology parameter estimates, we ran a sensitivity analysis for each species: We varied immigration rate, initial population size and fecundity, while holding all other parameters fixed. These parameters were varied because they are difficult to estimate, and previous theoretical work has shown that they may have profound effects on resistance evolution (Taylor and Georghiou 1979,

Tabashnik and Croft 1982). In the sensitivity analysis, we used 3 sets of parameter values for each species: (a) the mean estimated immigration rate (M), initial population size (P) and fecundity (F); (b) 10 M, 0.01 P and 0.67 F; (c) 0.01 M, 10 P and 1.33 F. The values in (b) are all altered to increase the predicted time to evolve resistance, whereas those used in (c) reduced the

predicted time to evolve resistance. Note that the ratio of (initial population size x fecundity) ÷ immigration, which can greatly influence predictions (Tabashnik and Croft 1982), was varied by a factor of 22,500 for each species in this sensitivity test.

For most species, the model's predictions were not greatly affected by the variation tested in the sensitivity analysis (see sensitivity bars for European red mite (Pu), codling moth (Lp), plum curculio (Cn), Fig. 4a). The predictions for some species, however, were greatly affected by the tested variation (e.g. Quadraspidiotus perniciousus, Fig. 4a).

The initial results for the 12 natural enemy species also showed a significant rank correlation between predicted and observed times to evolve resistance (Fig. 4b). Yet, for natural enemies, the predicted times to evolve resistance were consistently less than the historically observed times (Kolmogorov-Smirnov two-sample test, $p<0.05$). These results suggest that the original assumptions may omit factors which slow resistance development in natural enemies.

Two hypotheses not incorporated in the initial simulations have been proposed to explain why natural enemies evolve resistance more slowly than pests: (1) food limitation: a natural enemy evolves resistance only after its prey/host is resistant, because natural enemies starve, emigrate or their reproductive rate is greatly reduced following sprays which eliminate susceptible prey/hosts; and 2) pre-adaptation: pests are "pre-adapted" to detoxify pesticides because they detoxify plant toxins, but natural enemies are less "pre-adapted" (Huffaker 1971; Croft and Morse 1979).

To test the food limitation hypothesis we assumed that natural enemies began evolving resistance only after their prey/hosts became resistant. Therefore, to obtain predicted times for natural enemies, the observed times to evolve resistance for prey/host species were added to the original predicted times for each natural enemy species. This assumption substantially improved the correspondence between predicted and observed for all 6 natural enemies which were initially predicted to evolve resistance too fast. With the food limitation hypothesis incorporated, there was a highly significant rank correlation between predictions and observations for all species ($n = 24$, $r_s = 0.690$, $P = 0.001$).

We tested the pre-adaptation hypothesis by assuming that the LC_{50} of susceptible (SS) natural enemies was one-tenth that of susceptible pests' LC_{50} (Brattsen and Metcalf 1970, Croft and Brown 1975). This assumption did not substantially improve the correspondence between predicted and observed.

Although our test of the food limitation hypothesis oversimplifies the relationship between natural enemy-pest interactions and resistance evolution, the results support the view that food limitation following sprays is a major factor retarding resistance in natural enemies, whereas greater initial susceptibility may be less critical. This conclusion is consistent with experiments showing that a predatory mite (Amblyseius fallacis) which had 20 to 50-fold lower initial LC_{50} than its herbivorous prey mite (Tetranychus urticae) was able to evolve resistance rapidly when given an adequate food supply (Morse and Croft 1981). We emphasize, however, that the food limitation and pre-adaptation hypotheses are not mutually exclusive; their relative importance may depend on the species and pesticide.

In our simulation, species differed only in their population ecology parameters. Therefore, the significant rank correlations seen between predicted and observed times to evolve resistance suggest that ecological differences among species are sufficient to explain differences in rates of resistance evolution observed among apple pests and natural enemies. To further examine the influence of ecological factors on rates of resistance development, we tested for rank correlations between selected ecological parameters and observed times to develop resistance.

There was a strong positive rank correlation between the number of generations per year and the observed rate of resistance evolution ($r_s = 0.757$, $n = 24$, $P < 0.001$). Apple species with more than 3 generations yearly have evolved resistance to azinphosmethyl rapidly; those with 1-2 generations yearly have evolved resistance slowly or are not yet resistant. A similar relationship between generation turnover and resistance to aldrin/dieldrin has been reported for soil insects (Georghiou 1980). These findings support the modeling result (Tabashnik and Croft 1982) that the number of generations per year is important in determining the rate of resistance development.

Modeling has suggested that resistance will evolve more slowly as the ratio of susceptible immigrants to residents in the treated population increases (Comins 1977, Taylor and Georghiou 1979, Tabashnik and Croft 1982). The observed rate for resistance development was negatively correlated with the estimated ratio of immigrants:initial overwintering population size ($r_s = -0.584$, $P < 0.01$) and with the estimated ratio of immigrants:reproductive potential ($r_s = -0.692$, $p < 0.001$). These negative correlations support the idea that immigration by susceptibles can retard resistance development.

APPLICATIONS TO THE HORN FLY RESISTANCE PROBLEM

Horn fly resistance to insecticide-impregnated ear tags on cattle has been widely suspected and is documented for some populations (Quisenberry et al. 1984, Sheppard 1984, Schmidt et al. 1985). Application of simulation models to resistance problems with the horn fly will require basic data on ecological, genetic and operational factors. Progress should be facilitated by the considerable

amount of ecological data already available on the horn fly (e.g. Kunz et al. 1974; Palmer et al. 1981) and the existence of a horn fly population model (Miller 1977).

Key variables which may need to be studied include the genetic basis of resistance, spatial and temporal variation in pesticide dose, and immigration by susceptibles. Most models of resistance use single-locus genetics, but polygenic resistance to pyrethroids has been shown for some insect pests of medical importance (e.g. Culex quinquefasciatus, Priester and Georghiou 1979). Horn fly dispersal may be a key variable, because immigration of susceptibles can slow resistance development. Although additional data will be helpful, we can discuss resistance management strategies for the horn fly in light of information available now.

Horn Fly Ecological Parameters

Based on data from central Texas (Kunz and Cunningham 1977, Miller 1977), it appears that horn flies are active in substantial numbers from March through November. Their development rate is a function of temperature, with about 33 days from egg to adult required at a mean air temperature of 16°C (Miller 1977). Thus, with a mean of 16°C it seems likely that horn flies would complete at least 8 generations per year. In other agroecosystems, arthopod pests with many generations per year have been the fastest to develop resistance to pesticides (e.g. Panonychus ulmi, European red mite). The reproductive potential of the horn fly is reduced by relatively high "natural" mortality (greater than 97% from the egg to adult stages in some circumstances), but it is boosted by relatively high fecundity (200 eggs per female) (Miller 1977). Overall, the horn fly's ecological parameters suggest that it has high potential for resistance development, primarily due to its numerous generations per year.

Management Strategies

We have previously described a "high dose strategy" and a "low pesticide use strategy" for resistance management (Tabashnik and Croft 1982). The high dose strategy requires high levels of immigration by susceptibles and consistently high insectide doses to render the resistance gene functionally recessive (fig. 5). The high dose strategy is not appropriate for horn fly resistance management for several reasons. First, if large herds are treated with insecticide, then immigration of susceptible horn flies into a treated population may be low or nil. If there is not substantial immigration by susceptibles, a high dose strategy will cause rapid resistance development. Second, long insecticide half-life and spatial variation in dose cause exposure to intermediate doses in the field, even when a high dose is used initially. This type of variation in

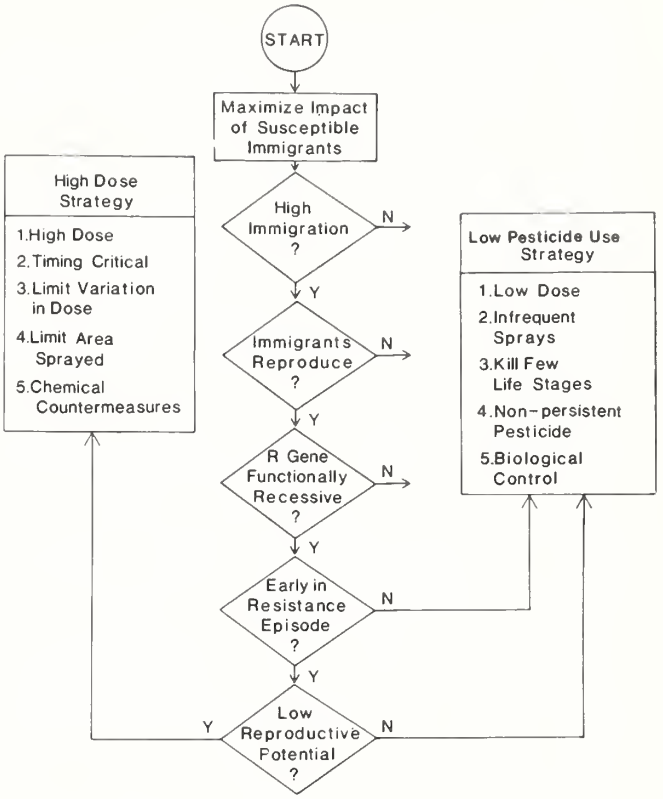


Figure 5. Flow chart decision scheme for resistance management (after Tabashnik and Croft 1982). The low pesticide use strategy is recommended for the horn fly.

dose can cause a high dose strategy to back-fire by promoting very rapid resistance (Taylor et al. 1983). Third, the high dose strategy is not likely to suppress resistance in insects with high reproductive potential, such as the horn fly.

The drawbacks associated with the high dose strategy suggest that a "low pesticide use strategy" would be more useful for retarding resistance in horn flies. This strategy might be implemented for horn fly resistance management by treating a reduced fraction of the herd, thereby allowing more susceptibles to survive. Because this strategy requires that more pests survive insecticide treatment, it is best implemented in concert with other control tactics as part of an integrated pest management (IPM) program. Sterile male release and biological control are potential alternative control tactics for the horn fly (e.g., Kunz et al. 1974).

The horn fly appears to be a good candidate for integration of biological and chemical control because its oviposition and development occur in manure, away from the cattle host where adult feeding takes place (Miller 1977). It seems that it would be feasible to combine partial control of adults by insecticidal ear tags on cattle with

biological control aimed at egg, larval and pupal stages off the host (Roush, pers. comm.). Insecticides typically eliminate natural enemies, but in this case, horn fly predators and parasites might be conserved due to their physical separation from the treated hosts.

In conclusion, some features of the horn fly problem do not give cause for optimism, but other aspects suggest that the horn fly may be amenable to resistance management. On the negative side, retarding resistance in the horn fly may be difficult because of the horn fly's high reproductive potential and because of the apparent lack of alternative hosts (Miller 1977) which might provide susceptible immigrants.

On the positive side, if moderate levels of horn fly populations can be tolerated, then reduced insecticide use is possible. Estimation of economic thresholds for the horn fly should be helpful in this regard. Several studies show weight gain disadvantages due to horn flies, but there also are conflicting results (see Quisenberry and Strohbehn 1984 and references therein). If horn fly populations are being controlled at levels below the economic threshold, then reduction in insecticide use may increase profits as well as retard resistance development.

Early recognition of increasing horn fly resistance to insecticides may be essential for finding solutions. We suggest that careful monitoring of levels of susceptibility to insectides be accomplished by standardized tests. Data on management practices and resulting changes in susceptibility levels could be used to evaluate control tactics and to test models of resistance evolution. Regional co-ordination of efforts to combat horn fly resistance may prove to be extremely useful both for accomplishing management goals and for advancing knowledge of resistance.

ACKNOWLEDGMENTS

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MODELS AS TOOLS FOR EXTENSION

John A. Jackman[1]

Introduction

This paper deals with the role of Extension in the delivering of computer based pest models. It discusses historical roles and future roles including case studies and philosophy of how pest models will be utilized. The information is of a general nature and is provided as ideas for Extension veterinary entomologists to consider. The case studies and examples rely by necessity on experience gained with crop pest models. The experience with crop pest models serve adequately as a guide for veterinary entomologists as they initiate pest models of their own.

The traditional roles of Extension are both adult education and public service. These dual roles by the Extension Service have the common objective to affect social change. Extension specialists are in a difficult and demanding role which requires a thorough understanding of research results, data limitations and needs of producers. Frequently, Extension personnel must weigh the control procedures and situation against probable outcomes based on research findings and provide a clear cut recommendation for action. This activity provides a great responsibility and a challenge due to various constraints on information available and on the communication process.

Computers have been promoted as a panacea for many agricultural applications (McGrann, 1983). Often a producer will ask that a computer provide all the answers. However, an equally common situation is a producer who has no idea what question to ask or sees no potential for this powerful tool. Identifying the area in between these views where computers can be useful remains an area for further exploration.

I am including a few comments about computers in general because models and computers are inextricably intertwined. The confusion occurs in the mind of users as well as the operation itself. Calculations and data tranfer take place inside a computer are obscure to the user. The complexity of the calculations or quality of research to support a model is totally invisible to the user.

Computers have many uses including communications, computation speed and information retrieval. The variety of software we create includes training aids, decision aids and record keeping applications. Some of the decision aids can be very complex simulation models which require more calculations than we could have imagined a few years ago.

In spite of these powerful computational applications we should not overlook the significance of the computer as an attention getter. The use of cathod ray tubes (CRT) as part of a computer brings together a familiarity and a sense of belief to a computer. Literally anything placed on the screen is likely to be accepted as legitimate with little question. This attention capturing ability and the sense of legitimacy are powerful salesmanship tools which should be recognized and utilized.

Models are a subset of computer applications and many models hardly require a computer at all. The strong points of a model are the ability to put facts together into a summarizing comprehensive package and the capability to evaluate anticipated new situations.

Model developers often have a variety of goals which may not all be compatible with Extension goals. Models that are created for a specific purpose seldom satisfy other purposes. This fact is frequently misunderstood by occassional model users. Each model can only be evaluated relative to specific objectives that were set as the model goals. If these goals are research goals we can not expect to use this directly in Extension applications. The transferring of research models to models useful by Extension is a major and serious undertaking. Models created directly by Extension personnel will often have pest control objectives and different structure.

Delivery of Model Results

The traditional use of a model was for a researcher to develop concepts and ideas from the model to direct his research. The researcher would supply information to Extension personnel who in turn relayed the information to the public (Figure 1). The Extension personnel fulfilled the role of summarizing and communicating information to the public.

The roles of Extension began to change when models became more complex, computer delivery systems more sophisticated and crop production economics more complex. Models became a framework for Extension thinking, allowing specialists to crystallize concepts mathematically. Specialists can use models to test their recommendations and to custom make recommendations more precisely than ever before. However, growers are becoming more demanding and often want to interact directly with the models themselves.

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Results from models are often available to growers in hidden ways. For example, simple economic thresholds are sometimes developed as a result of numerous computer runs. The results are available as just a rule-of-thumb, a graph or table of numbers. We easily forget that these are direct results from models.

Currently, researchers use models to summarize their work and help crystallize their thinking. The Extension specialist can use the model to indirectly access the thinking of researchers. This allows the Extension specialist to simply do a better job (Figure 2). An improved method of interaction with a model and both research and Extension specialists has naturally evolved in many cases.

Packaging

One aspect of models that is often overlooked is the fact that the complex information is difficult to digest. Many of the model inputs and outputs are very complex or labor intensive. Often the model has benefit if a prediction is made even without all of the inputs. The key point is that it is very critical to develop a good interface between a model and a user especially a grower (Figure 3). This interface needs to be developed carefully to assure user acceptance. A good job here can sell the product but a bad experience can cause rejection or create doubts about the quality of the overall project and research.

The job of building, designing and creating this interface is a task of packaging. This task has fallen mainly on Extension staff to complete. The primary requirements of the interface are relevance and ease of use. Relevance means that a model must fulfill a need. When a model was created for a research purpose, the model will require major revisions, changes or additions before the needs of a grower can be met. This effort in packaging must be recognized as an important distinct step and addressed that way. A research model can not be merely distributed to anyone without interpretation.

The ease of use of the application is a clever blend of good programming techniques, and carefully relating to the user. Each model needs the input and output designed to meet users needs, expectations and available data. Input should have prompt messages and menus to request all information. Help commands should be available at most points in the program as well as features to escape from the program. Certain program entry points should also allow for branching back in the program, storing data and an assortment of other features depending on the situation. Output should be available in several ways but always with the user's need in mind.

Case History of BUGNET

Computer use in Extension Entomology started in 1975 when the first bollworm and tobacco budworm (Heliothis spp.) predictions were made with the MOTHZV model and the data from the pest management programs were summarized with computers. Soon after, plans were made for a computer delivery system in pest management which was called BUGNET. Minicomputers were placed at locations with Extension entomologists around the State by 1977 and later reached a high of 14 machines. Extension entomologists have maintained an active project in support of pest management by using computers to predict the timing of pest occurrences, to support decision making, to deliver information, to analyze data and as a teaching tool.

Pest Predictions

A computer model entitled MOTHZV is used each year to predict the peak egg laying times for bollworm and tobacco budworm in cotton. Predictions are used by cotton producers to adjust scouting programs, avoid needless sprays, alter irrigation schedules and as an early warning for these pests. Predictions cover over 4 million acres of cotton and save producers several million dollars each year based on our informal survey.

The pecan nut casebearer, Acrobasis nuxvorella, a key early season pest of pecans, needs to be controlled in most orchards each year. Critical timing of scouting and spraying dates is predicted at about 60 locations across the State each season. These predictions have been more accurate than calendar date predictions which were traditionally used in the past. The target spray dates are distributed to producers through Extension media channels, i.e. newsletters and radio.

Other models are in various stages of development and delivery including ones for cotton plants, boll weevil, Southwestern corn borer and sorghum midge.

Decision Aids

Economic threshold levels have been used as standard rules-of-thumb for producers to know when to treat for pests. However, the decision to treat is a complex relation between pest density, crop stage, control costs and crop value. Software has been developed to customize calculations of economic levels based on information about pest levels from individual fields. Decision aids have been developed for sorghum midge, pecan weevil and leaf feeding caterpillars on peanuts.

Information Retrieval

Rapid access to information is another important area of computer use. Extension entomologists have developed a package to recall pesticide recommendations for most of the major crops in Texas. Another application provides information on the chemical compatibility of pesticides to be incorporated in a tank mix.

Difficulties and Pitfalls

Identification of needs is the most important part of developing a use for a model. Often we still develop applications based on what we think is desired or what we can do but miss the key element of need.

Packaging of the model in a useful way needs careful attention. The user's situation must be anticipated. The computer code must be carefully written to avoid causing fatal errors. A good testing program is critical to the success of model acceptance.

Maintenance of computer code is a continual problem. Each change in research may dictate a change in the pest model and every change in the model means a change in the computer code. When models become very complex and the number of models increases, maintenance problems increase drastically.

The maintenance problem is complicated by the rapid changes in the computer industry. Hardware, languages, operating systems and system configuration all create major problems for the maintenance of a model. The diversity of equipment and software make distribution and targeting software to various microcomputers very time consuming and difficult.

Future Plans

Our immediate plans are to make our existing applications more available. We will be converting our best applications into good reliable code targeted for the IBM-PC compatible machines. We plan to develop code for both MS-DOS and CP/M operating systems and we standardize on C (Kernighan and Ritchie 1978) as a language to increase portability.

We will build in many user friendly options that go beyond what we had before. New program standards defined for the entire Exension Service will be included. Code will be distributed as compiled code to anyone for a fee to cover handling costs and supplies. A distribution system has been set up in Extension to handle this.

In the long run, individual models will be the main-stay of our computer applications. Long range plans are to include information recall applications, decision aid and models into a more integrated access system.

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McGrann, J.M. 1983. Microcomputer Software Development and Distribution. Southern Journal of Agricultural Economics. July.

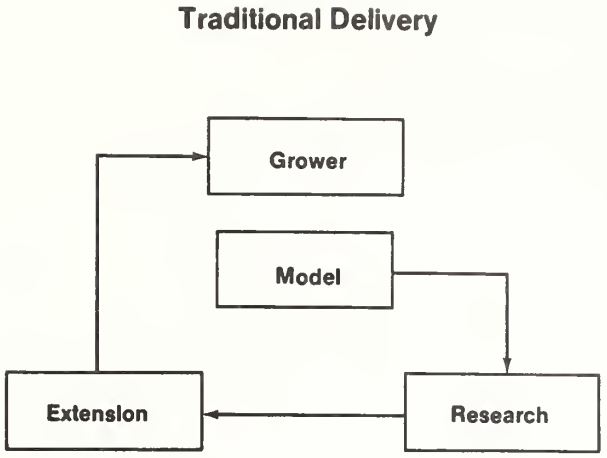

Figure 1. Traditional delivery scheme for model information.

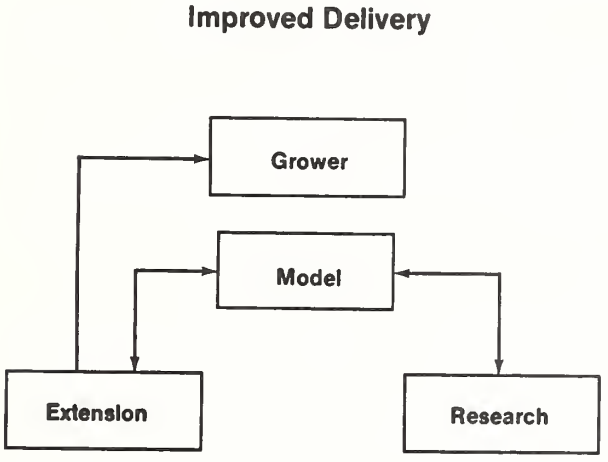

Figure 2. Improved delivery scheme for model information.

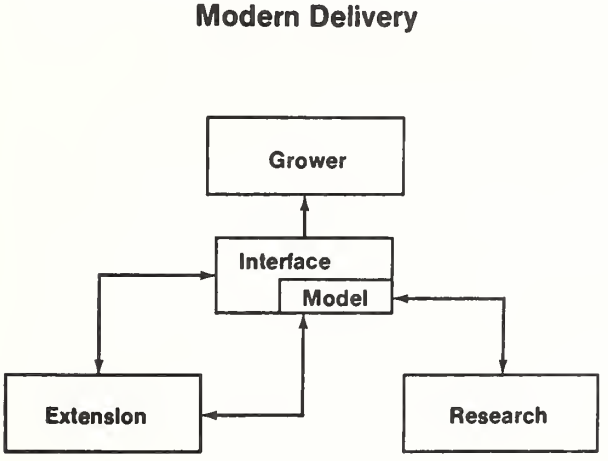

Figure 3. Modern delivery scheme for model information.

STRUCTURE AND VALIDATION OF FLYPOP: A SIMULATION MODEL OF FACE FLY POPULATIONS

R. D. Moon[1/]

Introduction

Since arriving in North America, the face fly, Musca autumnalis DeGeer, has been studied extensively in the laboratory and field (Pickens and Miller, 1980). Despite a wealth of detailed knowledge, producers are unable to adequately manage populations of the fly with available control measures. Part of the difficulty may be inherent in existing chemicals and formulations, and part may be due to our lack of understanding of the biology of the fly-cattle-pasture life system.

As outlined elsewhere in this workshop, simulation modeling is one vehicle for understanding complex biological systems. I have adopted the modeling approach in my research on face fly populations, and have constructed a computer model I call FLYPOP. This paper is a status report describing its structure and underlying assumptions. I will also describe efforts to validate it with laboratory and field data.

Design Objectives

FLYPOP was designed with the following objectives in mind:

1. The model should integrate knowledge of biological processes and relationships governing populations in the field.
2. It should account for observable demographic changes throughout the fly's reproductive season; that is, the model should predict seasonal trends in numbers and age structure from first appearance in spring to disappearance in fall.
3. The model should simulate fly populations at different locations and in different years with a minimum of external site specific data.
4. It should be realistic and thereby provide a means of simulating practical control experiments.
5. The model should be detailed enough to accommodate future work on the epizootiology of bovine or equine pathogens.

Structure of FLYPOP

FLYPOP simulates the weather-driven dynamics of a face fly population within a single grazing unit at a specific site and year. The weather is described by an external file of sequential minimum and maximum air temperatures as available from NOAA. Other meteorological characteristics such as rainfall, wind, saturation deficit and solar radiation are ignored.

System Compartments

The grazing unit has unspecified but fixed spatial dimensions, and contains a constant but unspecified number of cattle and their cowpats. The unit is conceptually divided into three fly habitats: fly overwintering sites, cattle and surrounding vegetation, and cowpats with underlying soil and duff. Each has a different microclimate. The overwintering sites are occupied by overwintering flies in diapause. The second contains reproductive adults which experience ambient air temperatures. The dung-soil habitat contains the immature stages, egg to pupa inclusive, which experience slightly warmer temperatures. Movement from the immatures' habitat to the adults' habitat is implicit in eclosion of adults from puparia. No provision is made for spatial movement of reproductive adults among cattle, cowpats and surrounding vegetation. Furthermore, net movement of flies out of and into the grazing unit is assumed to be zero and independent of fly age.

Calendar, Clock and Weather

A simulation runs from an initial Julian day (JD) to a final JD as specified by the user. During each day, the model computes the daylength and times of sunrise and sunset using a trigonometric function of site latitude and the solar angle at sunrise and sunset (Appendix 1).

Each day from midnight to midnight is divided into 5 periods (timesteps) designated as NITE1, DAY1, DAY2, DAY3, and NITE2 (fig. 1). NITE1 begins at midnight and ends at sunrise. DAY1 ends at noon. DAY2 ends 5 hours before sunset. DAY3 ends at sunset, and NITE2 ends at midnight. As the times of sunrise and sunset vary with latitude and JD, so do the durations of all timesteps except DAY3.

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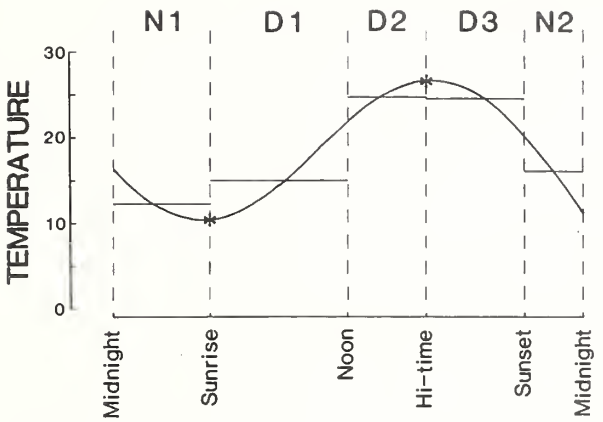

Figure 1. Daily clock and temperature as modeled in FLYPOP. A day is divided into 5 timesteps separated by the times designated along the X axis. Sunrise, hi-time and sunset vary with Julian day (Appendix 1). Reported minimum and maximum field air temperatures (asterisks) used to drive the model are assumed to occur at sunrise and hi-time, respectively. Mean temperatures (horizontal lines) during each timestep are computed according to the algorithm in Appendix 2.

Daily minimum and maximum air temperatures are read in sequence from an external file as the simulation progresses. The minima are assumed to occur at sunrise (the end of NITE1) and the maxima at hi-time (the end of DAY2). The model computes the average air temperature during each timestep from a trigonometric function of an appropriately ordered pair of temperatures and the times for the beginning and end of the timestep (fig. 1 and Appendix 2). Dung temperatures are inferred from corresponding air temperatures (Moon, 1983), and similarly integrated to estimate the average during each timestep.

Life Stages

The basic demographic unit in FLYPOP is a cohort (fig. 2), a group of individuals originating during a given calendar day, either as females emerging from overwintering sites in spring or as eggs from other cohorts once oviposition has begun. The individuals in each cohort are further sorted into one or more of seven possible life stages (fig. 2): immatures and six classes of adult females. A sex ratio of 1:1 is assumed and males are ignored once emerged.

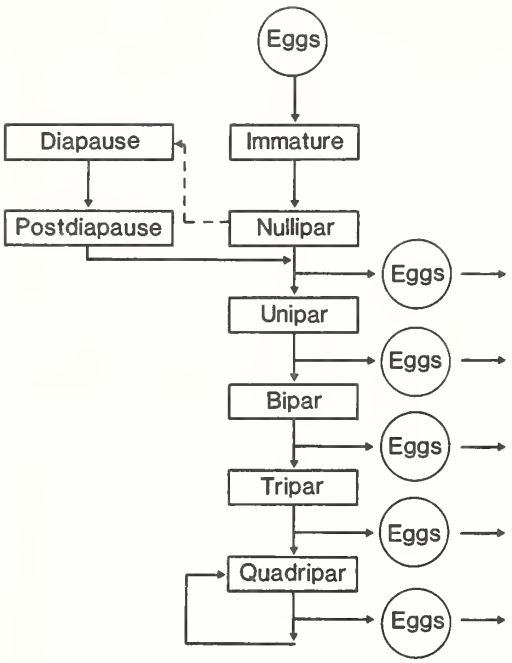

Figure 2. Life stages of face fly as modeled in FLYPOP. Dashed line between nullipar and diapause stages indicates process currently missing from the model. Eggs are collected from all cohorts old enough to lay them and are entered as immatures in the current JD's cohort.

Exodus From Diapause

All flies are assumed to be in diapause at the beginning of the year. They can emerge from overwintering sites (OWS) during DAY2 of any day on or after 1 March (JD 60), a presumed date when diapause has terminated. If females are present in OWS and the day's maximum air temperature exceeds a flight threshold of 10°C, then 25% of the flies in OWS are moved during DAY2 to the postdiapause stage. This process is repeated each day until all females are out of OWS. Thus, the exodus from diapause is modeled as a gated, exponential decay process that produces several cohorts of postdiapause females in spring. The cohorts' calendar ages depend on the temperature after 1 March. Intermittent warming above 10°C spreads them out in time.

Reproduction

Postdiapause females possess lipid-rich hypertrophied fat bodies which distinguish them from 0-pars (fig. 2). Females in both stages advance reproductively through a series of gonotrophic cycles. Each cycle culminates with the laying of 29 eggs and transition to the next stage. A negligible fraction can survive to be recycled through the quadriparous stage. All females are implicitly assumed to mate during the postdiapause or 0-parous stage.

Aging

Developmental times of all stages are modeled as temperature-dependent distributed delay processes with additional delays governed by the daily clock. Within each cohort, individuals in each stage have a mean fractional physiological age (MFA); ages of immatures and 0-pars range from 0.0 to 1.0 and beyond, whereas those of postdiapause, 1-pars and subsequent stages range from 0.285 to 1.0 and beyond. The latter difference accounts for previtellogenic growth of primary follicles that occurrs during the preceeding fall in females that overwinter, and of penultimate follicles during all other reproductive stages.

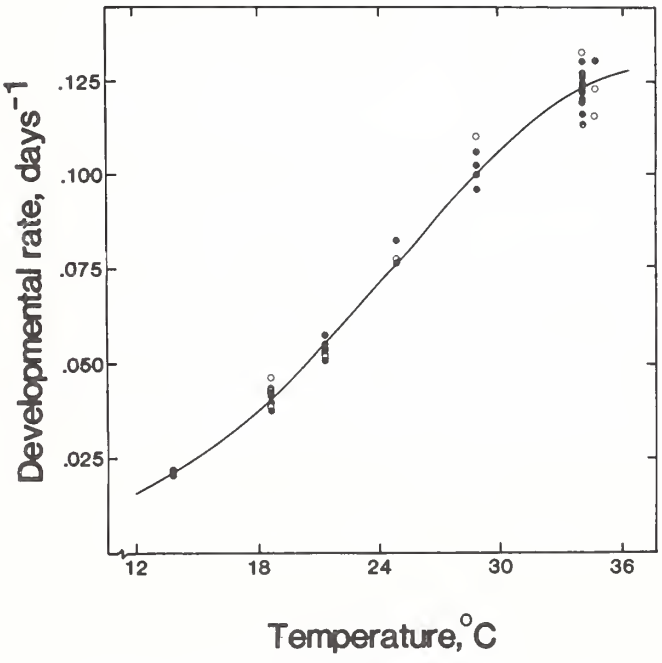

Figure 3. Developmental rate from egg to adult vs. constant temperature (T) as observed (points) and least squares regression line: Y = EXP(-6.482+0.2346T-0.0031T^2)(Moon, 1983).

Increase in MFA for immatures during a given timestep is a curvilinear function of dung temperature (fig. 3), whereas that of the females is a jointed linear function of air temperature (fig. 4). Transition of individuals from one stage to the next is distributed in time according to the algorithm presented by Sharpe et al. (1977). Eclosion of adults is gated to NITE1, DAY1 and DAY2; i.e., adults emerge from dawn to hitime only. Eggs can only be laid during DAY1, DAY2 and DAY3.

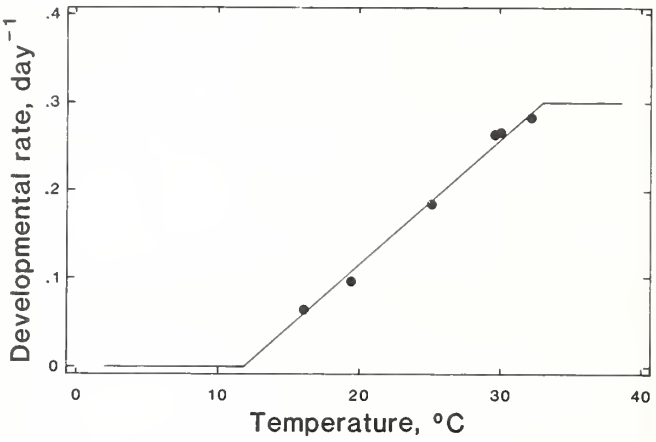

Figure 4. Mean developmental rate from emergence to first oviposition vs. constant temperature (T). At least 20 isolated females were reared per temperature. Least squares line is Y = -0.169+0.0143T. The females' developmental rate is assumed equal to 0 at temperatures below 11.82, and equal to 0.30 at temperatures above 32.8.

Survival

Survival of females from one timestep to the next is partitioned into three independent components (Appendix 3). A background daily survival rate of 0.925 is solely time dependent. A second time dependent component (fig. 5) is related to heat, where air temperatures above 27°C decrease survival (Turner and Hair, 1966). The third component is related to extremely cold air temperatures. Survival is 0.0 if the minimum is -5°C or below. All females except those in OWS are at risk to death due to background causes and heat, whereas only the 0-par to 4-par stages are at risk to freezing.

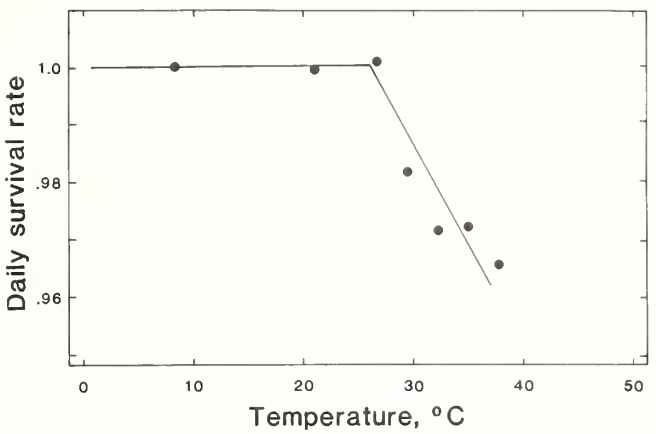

Figure 5. Daily survival rate of females reared at constant temperatures (T) by Turner and Hair (1966). Each point represents average survival during the first week of their experiment, after correcting for a background death rate of 0.968 per day at temperatures below 27°C. The resulting survival function is Y = 1.0 per day at temperatures below 27°C, and Y = 1.0099-0.00368T per day when above.

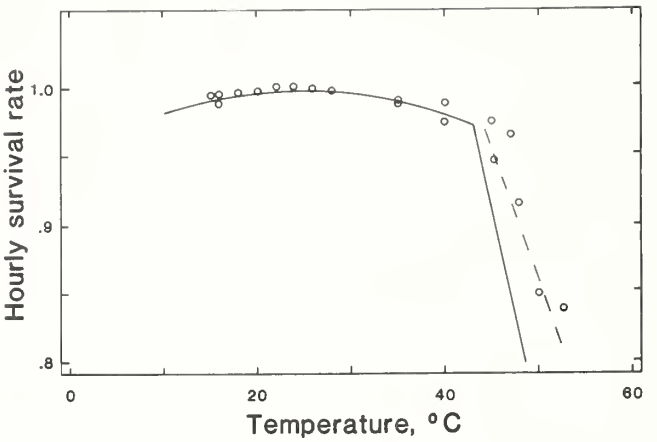

Figure 6. Data from Valiela (1969) and piecewise function relating dung temperature (T) to hourly survival of eggs, 1st and 2nd instar larvae of face flies (MFA < 0.1364). Horizontal curve given by Y = 0.9527 + 0.00385T - $0.000078T^2$. At T > 42.19, Y = 9.4 - 0.2T per hour. Departure of descending limb from data was compelled by summer field experiment (fig. 10) where no 1st and 2nd instar larvae survived to pupate following afternoon dung temperatures hotter than 47°C.

Survival of immatures is also divided into separate components (Appendix 4). A background stage specific survival rate of 0.8 is applied to mimic egg infertility and other unknown causes of death as observed in laboratory cultures (Moon, 1980; Valiela, 1969). A second component depends on dung temperature (fig. 6). Those below -1°C kill all individuals. Temperatures between -1 and 42°C cause comparatively little mortality, whereas those above 42°C are relatively severe. A third component attributed to predation is set at a seasonal constant of 0.5 (Thomas et al., 1983; Valiela, 1969). Eggs, 1st and 2nd instar larvae are at risk to predation and heat stress, whereas 3rd instar larvae and pupae are assumed immune to both. Survival of all larval instars is assumed to be independent of their density.

Diapause Induction and Development

At present, knowledge is not sufficient to model diapause induction and development during fall. Field samples from pastures in California, Iowa, and Minnesota and elsewhere suggest that at least some flies develop into diapause as early as the first week in September (Kaya and Moon, 1978; Krafsur et al., in press). Growth chamber experiments to describe the underlying processes have been completed (Read, 1984) and the resulting mathematical relationships will be added to FLYPOP in due course.

Program Flow

The major demographic variables maintained during a simulation are depicted in figure 7. At any time, cohorts can exist of calendar age 0 (arising during the current JD) or older. The numbers of individuals in existing cohorts are sorted by life stage. Those in each life stage have an associated mean fractional age (MFA). Finally, the distributed movement from one stage to the next is facilitated by a third variable, percent advanced.

The sequence of events and processes during a simulation is depicted in figure 8. "Setting up variables" involves zeroing the population matrix, opening the weather file, reading and computing the initial step temperatures, and setting the calendar and clock. An arbitrary number of females is placed in OWS. The heart of the model is contained in a loop of computations, starting at hi-time on the initial day and repeating with each succeeding timestep until the season ends as defined by the user.

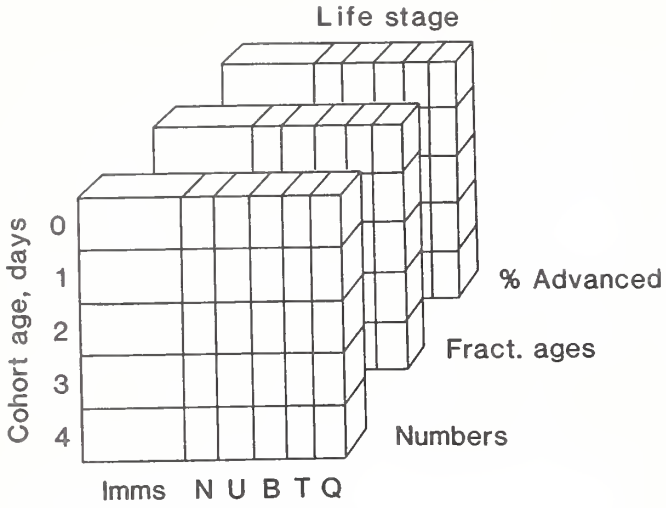

Figure 7. Matrices in FLYPOP used to represent numbers, mean fractional ages, and percent of those in each cohort's stage having advanced to the next stage (Sharpe et al., 1977). Imms, N, U, B, T, Q represent immatures, 0-pars, 1-pars, 2-pars, 3-pars, and 4-pars, respectively.

Diapause flies are moved as described above. Next, potential age increments for immatures and females are computed, as are temperature, time and age specific survival rates. The survival values are then applied to the population matrix before MFAs are increased. Eggs are collected from all females whose updated MFAs indicate transition from one parity class to the next. Forward transitions of numbers are then made. Finally, the population can be censused at the user's request to extract demographic statistics of interest such as total females present, the proportion of them that are parous, and so forth. FLYPOP is currently coded in Pascal and is available on request.

Validation

Efforts toward validation thus far with independent data sets have included experiments to check the aging and survivorship functions for the immatures, and a longitudinal field study where the model's overall performance was compared with observed trends in abundance and age structure.

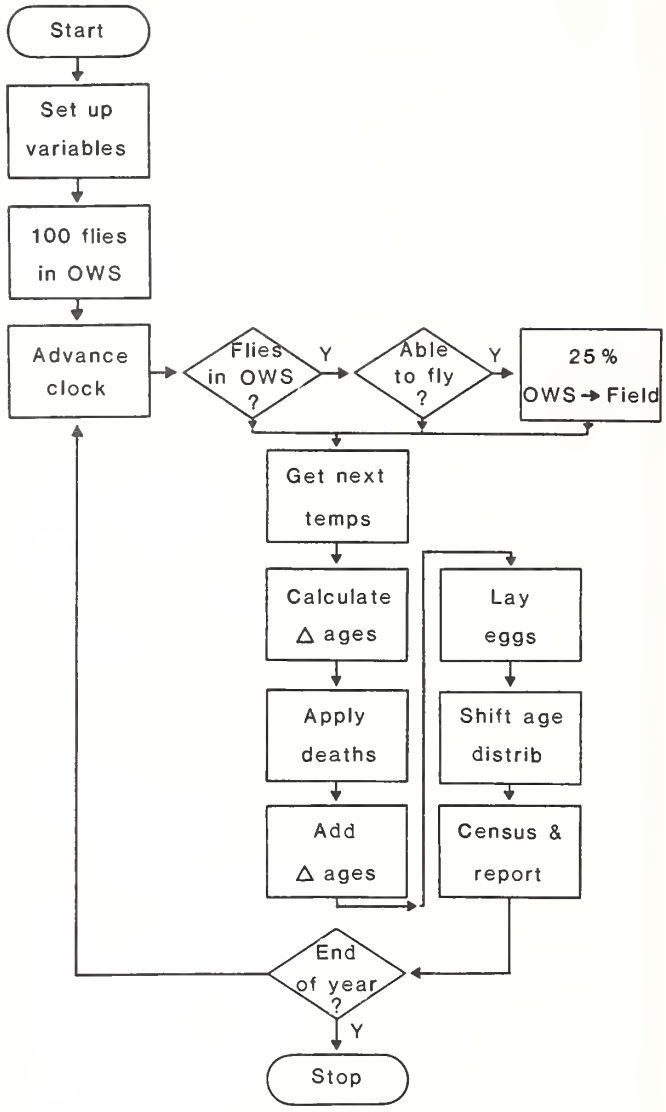

Figure 8. Flow chart of FLYPOP depicting the order in which the major population processes are simulated.

Aging and Survival of Immatures

The abilities of FLYPOP to predict midpoint developmental time and survival from egg to adult were examined by placing groups of 200 freshly laid eggs in 2kg dung pats. Four pats each were placed in growth chambers with three different fluctuating temperature regimes (Moon, 1983). Similar pats with eggs were transferred into the field in St. Paul, MN, during a

succession of dates in fall, 1981 (Moon, 1983), and pairs of pats were transferred during spring and summer, 1983. Field predators were excluded with fine screen, and the dung temperatures in selected pats were measured at minute intervals with a Campbell Scientific CR21L data logger.

Observed times from oviposition to emergence of the first, midpoint and last adults were then compared to the times of emergence as predicted by FLYPOP given the dung temperatures. The results (fig. 9) indicated that agreement among observed and predicted median developmental times was very good (R^2=0.97) and unbiased over a wide range of predicted developmental times. Agreement with times to first and last emergence was similarly good.

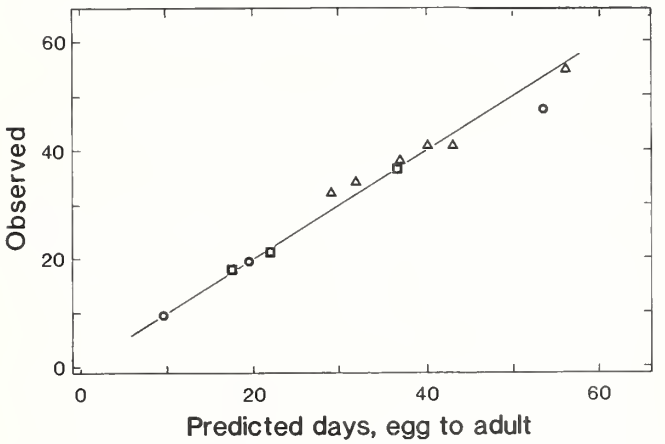

Figure 9. Comparison of observed and simulated days from egg to midpoint emergence of adult face flies reared from 2kg cowpats housed in growth chambers or in the field. Simulations based on daily min and max temperatures recorded in the dung. Circles, squares and triangles represent data from growth chambers, fall 1981, and spring 1983, respectively. Diagonal line represents perfect agreement.

Predictions of percent survival in the absence of predators (fig. 10) were also unbiased over a wide range of temperature, although substantial variation in observed survival remained unexplained (R^2=0.58). Often, great differences occurred between pats transferred to the field on a common date. This is thought to be due to experimental technique rather than failure to the survivorship functions for immatures.

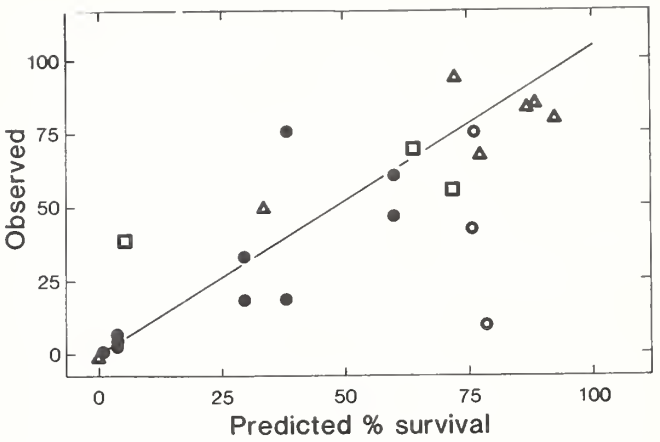

Figure 10. Comparison of observed and simulated survival from egg to adult given daily min and max dung temperatures as in figure 9. Screen enclosures excluded predators in the field. Squares, open circles and triangles represent data from chambers, fall 1981, and spring 1983 in St. Paul. Filled circles represent data from summertime experiments used to adjust the descending limb of survival function in figure 6.

Field Population

Performance of the complete model has been examined by running the model with sequential min-max temperature records from a weather station near a field site where a face fly population was routinely sampled. Model output for the site-season was then compared with sample data from the corresponding study population.

The field data set was from Wabasha Co., MN, in 1982. The set consists of a series of catch rates and measures of proportions parous on 29 dates from 27 April to 15 October. On each date, at least 10 and often more cylindrical white sticky traps (Kaya and Moon, 1978, fig. 1) were set up for several hours in occupied pastures to trap female face flies. An index of abundance was derived by computing females trapped per hour of standardized trap effort (Moon and Kaya, 1981), and then averaging over traps from the same day.

The proportion of the females that were parous on each sampling day was estimated by dissecting and age grading (Van Geem et al., 1983) the trapped flies and supplemental flies netted from cattle and a nearby blood smeared board. Fecundity was checked by measuring flies' head

widths and estimating mean eggs per cycle with the formula Y=-21.25 + 18.17X, where X is mean width in mm (Moon, 1980).

The field data and FLYPOP output were compared as follows. In the absence of a routine to model diapause development and movement to OWS, evaluation was confined to the part of the season when dissections indicated that diapause was not occurring. The model was simply "turned off" on the JD when diapausing flies first appeared in the field.

Numbers of flies in the model are in unspecified units of abundance, whereas field abundance was measured as flies per standard trap hour. If one could translate catch rates (or face counts) into absolute numbers present in a population and also express numbers in OWS in late winter the same way, then comparison would be straightforward. However, this is not presently possible.

As an alternative approach, FLYPOP numbers were related empirically to the catch rates in the field by estimating a single calibration coefficient via least squares regression of observed catch rates (Y) on FLYPOP numbers (X) for corresponding sample days, using a line forced through the origin. In essence, the method assumes that catch rates and total females in the model are both linearly related to total population size. Interpretation of results, then, is correctly focused on the magnitude and timing of relative changes in abundance. Since the proportion parous is unitless, i.e., a fraction of the total females present in the field and in the model, the two can be compared directly.

The results from Minnesota are presented in figure 11. Flies were trapped from the first sampling date to the last, with an erratic, almost exponential increase to a peak of 10.8 on 25 August (JD 237), just before diapause was first observed on 2 September. The precipitous decline thereafter is thought to be the result of diapause and attendant emigration from the sampled area.

Seasonal abundance as predicted by FLYPOP driven with temperature records from the nearest NOAA station (Theilman, MN, 6 km SE of the field site) was in remarkable agreement. Model flies emerged shortly before the first sample date and were continuously present until 31 August. Abundance increased as observed in the field samples. The timing of the increase corresponded well with that observed, although the model seemed to be running slightly behind the field population.

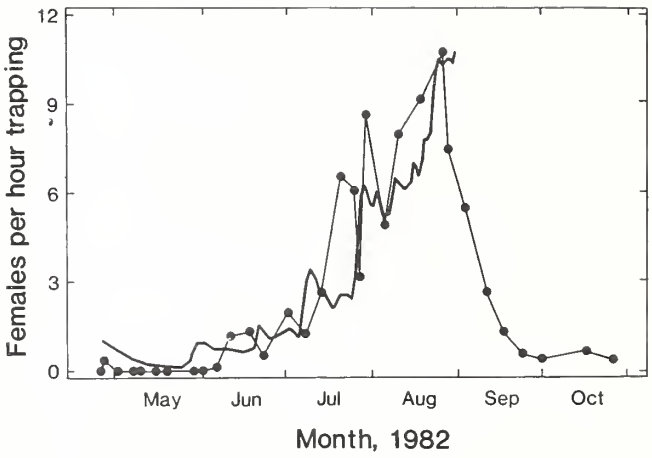

Figure 11. Observed and simulated catch rates for the field population of adult female face flies in Wabasha Co., MN, 1982. Connected points represent observed catch rates and the bold line is model output. Scaling factor of 0.0325 was used to adjust FLYPOP output. Spearman's r = 0.93.

The observed and predicted age structures of the females are presented in figure 12. Field samples were initially all postdiapause and made the transition to all parous by 15 May (JD 135). Recruitment of F1 females was evident on 29 May (JD 149) from the abrupt decline in proportion parous. From then onward, proportions parous oscillated with decreasing amplitude toward a value of 0.35. Proportions parous predicted by FLYPOP behaved quite similarly, with the exception that the second peak was neither as early nor as broad as observed in the field. This discrepancy appears to have resulted in a phase shift to the right in the predicted proportions parous thereafter. The reason(s) for the discrepancy is unclear. It may be related to the model's description of the process bringing females out of OWS, and perhaps to an inadequacy of our understanding of springtime survivorship and developmental times.

Comparison of age structure (fig. 12) with abundance (fig. 11) allows further interpretation of the observed pattern in the catch rates. Population growth at the Minnesota site seems to be accounted for simply by the temperature related survival, reproduction and growth of an initially synchronized group of diapausing females. Judging from the cycles in proportions parous, at least five major waves of reproduction occurred. An interesting feature of this hypothesis is a predicted age structure

bottleneck in spring, and a predicted convergence toward a stable stage distribution which apparently is not obtained because diapause intervenes at the end of August. Carey (1982) and others have noted that such oscillations follow from growth and reproduction by a group of colonizing females.

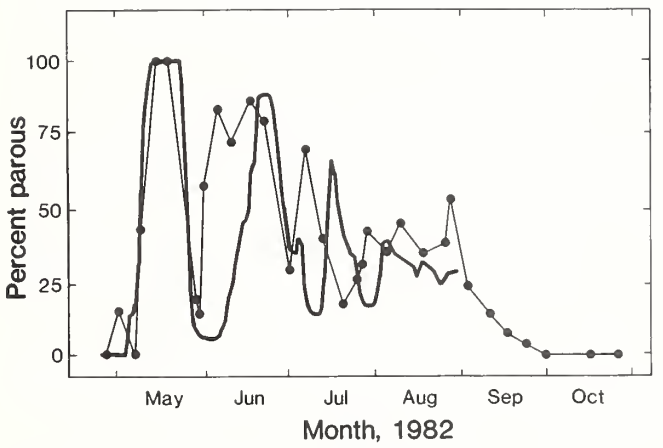

Figure 12. Observed and simulated proportions parous for adult female face flies in Wabasha Co., MN, 1982. Connected points and bolder line as in figure 11.

Discussion

The process of building and validating FLYPOP thus far has focused my attention on three gaps in our knowledge of face fly's biology. The first concerns the mechanism(s) that brings the females out of OWS in spring. The ad hoc assumptions described earlier seem to produce patterns indistinguishable from field observations. Dr. E. S. Krafsur at Iowa State University has an extensive set of data spanning 5 seven successive springs in Iowa (Krafsur, Moon and Church, 1985), and Dr. E. T. Schmidtmann of ARS has a set from one spring in Maryland. Each has made them available for analysis. I have found that FLYPOP does as well at predicting the dates of first springtime ovipositions, first 50% parous, and first F1 emergence for the flies in Iowa and Maryland as it does for the flies in Minnesota.

The second gap concerns the magnitude of predation, currently set at a constant 0.5 for egg to the end of the 2nd instar. I suspect that predation varies both geographically and seasonally, but there is only one careful seasonal field study (Thomas, et al., 1983) from which to judge the magnitude of predation.

The third gap is in our understanding of diapause induction, development and emigration from pastures. As noted earlier, progress in this area has been made by one of my students, and this gap may soon be filled.

Despite these deficiencies, FLYPOP did a very good job of accounting for face fly population trends during one season in southeastern Minnesota. As further validation work and sensitivity analyses are completed, additional refinement will surely be necessary. The model is a convenient tool for establishing the direction of future research, and the structure of the model will allow simulation of alternative control measures and studies of the epizootiology of bovine pathogens.

Summary

A computer simulation model called FLYPOP has been developed to aid in the field study of face fly populations, Musca autumnalis DeGeer. The model is a process oriented, deterministic program driven by an external file of min-max air temperatures as commonly reported by NOAA reporting stations. The model describes the dynamics of an age-structured fly population from early spring to late summer within a closed grazing unit containing a constant number of cattle.

A simulation begins in late winter with an arbitrary number of females in overwintering sites. Based on the weather, the model simulates the emergence and subsequent development, survival and reproduction of cohorts of females having emerged on separate days in spring. Cohorts of offspring, each arising as eggs during a given day are also maintained separately. Immatures develop through a single age class (egg to pupa inclusive), whereas females can develp through five gonotrophic cycles, each ending with the laying of eggs. Diapause development and emigration from pastures in fall are not presently described.

Validation has involved small rearing experiments to check selected parts of the model, and a longitudinal field study of a wild population to compare with the model's overall performance. Experiments have consisted of rearing immatures in dung pats placed in growth chambers and in the field. Observed developmental times and rates of survival from egg to adult were compared with the same statistics as predicted by the model given the temperatures actually experienced by the experimental flies. Model output agreed quite well with the observed data.

Catch rates and proportions parous of females on white sticky traps were available from a dairy in Wabasha Co., 1982. The former is a measure of female abundance, whereas the latter is a measure of their age. FLYPOP was run with sequential min-max air temperatures from Theilman, MN. Observed and predicted numbers agreed closely with the population, exhibiting exponential growth during the months of June-August. Observed and predicted age structures oscillated toward a stable stage distribution in August. The model seemed to be an adequate descripion of the observed dynamics in the field and is a vehicle for further research on control methods and epizootiology of cattle and horse pathogens.

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Appendix 1

This algorithm was worked out by Dr. J. Witz, ARS, College Station, TX. On any Julian day (JD), the solar declination (DEC) is approximately

$$DEC = 23.44*COS(0.9685*(JD-172)).$$

When combined with site latitude (LAT) and twilight angle (TWI), both in degrees, the daylength in hours is

$$DL = (2/15)*ARCCOS\left[\frac{SIN(TWI)-SIN(DEC)*SIN(LAT)}{COS(DEC)*COS(LAT)}\right]$$

A value of -0.833 for TWI corresponds with astronomical sunrise and sunset, the angle between the center of the sun, the observer and the horizon when the upper limb of the sun is at the horizon. Times for sunrise and sunset on a given JD are approximated by centering the daylength on either side of local solar noon,

$$sunrise = 12 - 0.5*DL$$

$$sunset = 12 + 0.5*DL.$$

Appendix 2

The following algorithm yields a mean timestep temperature and was derived by integrating and then averaging the half cosine functions given by Regniere (1982). The timestep can occur during an increasing temperature phase between sunrise and hi-time (DAY1, DAY2) or a decreasing phase between hi-time and the next day's sunrise (DAY3, NITE2, NITE1)(fig. 1).

The temperature, T, at a specific time of day, t, in fractional hours, is estimated from

$$T = C_1 + C_2 * COS(\pi (t-a)/b)$$

where T1 and T2 are the temperatures at the start and end of the appropriate phase, C1 = $(T_1+T_2)/2$, and C2 = $(T_1-T_2)/2$. t is hours from midnight to the time of interest, a is the time of day when the phase began, and b is the length of the phase, all in fractional hours.

By integrating and solving for a mean T between t-Δt and t, one obtains

$$T = C_1 + C_2 * \frac{t-a}{\pi * \Delta t} * \left[SIN\left(\frac{\pi * (t-a)}{b}\right) - SIN\left(\frac{\pi * (t-a-\Delta t)}{b}\right)\right].$$

Appendix 3

The principal assumptions underlying the method for estimating females' survival during a timestep are that deaths can be due to separate but independent causes, and that the component probabilities of surviving are constant during the timestep.

Survival from the beginning to end of a timestep is given by

$$S = S_b * S_t * S_f$$

where

S_b = survival from "background" causes of death, $= (0.925)^{\left(\frac{\Delta t}{24}\right)}$, Δt in fractional hours (see Krafsur, et al., 1985); S_t = 1.0 for mean step temperatures (T) between -5 and 27°C, or $= (1.09939-0.00368*T)^{\left(\frac{\Delta t}{24}\right)}$ for T > 27°C (fig. 5);

S_f = 0.0 only during NITE1 if the minimum air temperature at sunrise is below -5°C, or = 1.0 otherwise. The number of females in a chosen group surviving the timestep is given by

$$N_t = (N_{t-\Delta t}) * S.$$

Appendix 4

The method used for computing survival of immatures parallels that used for females:

$$S = S_b * S_t * S_p * S_f$$

where $S_b = (0.8)^{\Delta MFA}$, with ΔMFA being the increase in mean fractional age associated with T during the timestep; S_t = the temperature-dependent hourly survival rate (fig. 6), adjusted to a daily basis;

$S_p = (0.5)^{\left(\frac{\Delta MFA}{0.1364}\right)}$, for individuals whose MFA < 0.1364, i.e., younger than 3rd instar, or = 1.0 otherwise; and S_f = 1.0 if T > -1°C, = 0.0 otherwise. Numbers of immatures in a chosen cohort surviving to the end of the timestep are

$$N_t = (N_{t-\Delta t}) * S.$$

MODELING AND SIMULATION OF STABLE FLY POPULATIONS

Ivan L. Berry[1/]

Introduction

Existing models of stable fly, Stomoxys calcitrans (L.), populations are based on estimates of average rates of development, mortality and reproduction for constant environments. Functional relations among key variables have been established for some of the components, but other important variables cannot even be measured. Therefore, current models of stable fly populations may be classified as incomplete component models (Southwood 1978), and future advances in model development depend on continuing life history research and analysis.

Overview of Existing Stable Fly Models

Population models were developed by LaBrecque et al. (1975) and Weidhaas and Haile (1978) using constant rates of mortality and reproduction for constant environments. Dynamic models of life table components were developed to describe such factors as immature development vs. temperature (Berry et al. 1976, Kunz et al. 1977, Berry et al. 1977), adult mortality vs. temperature (Berry and Kunz 1977), oviposition rates vs. temperature and humidity (Berry and Kunz 1978), adult mortality at cold temperatures (Beerwinkle et al. 1978) and overwintering behavior of immatures (Berry et al. 1978). Efforts to indirectly measure adult mortality have resulted in behavioral models which may ultimately be incorporated in more comprehensive population models (LaBrecque et al. 1975, LaBrecque and Weidhaas 1975). Most of the above models were generated entirely from laboratory data and were not validated in the field. Physiological variables, such as development rates, may consistently depend on temperature, so that field applications depend only on the ability to measure or predict habitat temperatures. The form of some laboratory-derived models may be entirely adequate if the values of coefficients can be determined for field environments. Behavioral components may need to be quantified almost entirely in the field.

Numerous methods for estimating and describing population parameters are available (Seber 1973, Southwood 1978). Nevertheless, the lack of quantitative information about several components of the life table of stable flies is the major barrier to the rapid development of more comprehensive models.

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Structure of a Proposed Model

Life stages to consider in a comprehensive stable fly model are listed in Table 1. Transitions between stages are listed separately because mortalities at those times may vary substantially from those occurring in the adjacent periods. Examples include the possible susceptibility of emerging adults and ovipositing females to predation. The various activities associated with the mobile stages may all have a direct bearing on the intrastage survival. Dispersal and oviposition are also important inputs for subsequent generations. Feeding behavior is an important model output because it is almost solely responsible for the economic impact of stable flies. Finally, some of the activities, such as feeding, provide the most practical means of assessing population size and monitoring populations for control programs.

Table 1. List of stages, events and activities of female stable flies for possible inclusion in comprehensive models.

		Activity	
Stage	Input Event	Feeding	Reproduction
Egg	Oviposition	-	-
Larva 1	Hatch	Cont.	-
Larva 2	Molt	Cont.	-
Larva 3	Molt	Cont.	-
Pupa	Pupation	-	-
Adults			
Nulliparous 0	Emergence	Initial	-
Nulliparous 1	Post-Emer.	Feeding	-
Nulliparous 2	-	"	-
Nulliparous 3	-	"	Mating
Nulliparous 4	-	Periodic	-
Nulliparous 5	-	Feeding	Oviposition
Uniparous 3	Oviposition	"	-
Uniparous 4	-	"	-
Uniparous 5	-	"	Oviposition
Biparous 3	Oviposition	"	-
"	"	"	"

The components listed in Table 1 can be represented with a computer model rather simply by defining a table that contains the numbers of individuals within narrow age ranges. Increased precision can be obtained by expanding the table into narrow ranges of a continuous scale of development in a second dimension. Such a table would represent the current status of a population, and the transitions during each time increment would be simulated by shifting or summing numbers to the appropriate cells and decreasing them according to estimated mortality. These transitions are easily modified to represent the effects of the environment during the time increment. Supplementary tables may be used to accumulate egg production and a measure of feeding activity during the time increment, and additional

tables may be used to hold relative measures of size, nutritional status, or other factors that might affect the same cohorts in later stages of development.

Key factors which are not listed in Table 1 may include resting behavior, movement or migration, dependence of survival on population density, and the effects of control practices. Within areas where stable flies are a chronic problem, the tendency to use control measures on larger populations may be a form of density dependence.

Submodels of Individual Components

The complexity of the comprehensive model described above obviously requires that individual components be intensively examined. If certain of the individual components are similar, or cannot be isolated, then they may be lumped together for analysis. Those components which provide opportunity for close study of the population dynamics, such as feeding and oviposition, have and will continue to receive detailed attention. Less obvious components, such as the mortality of first instar larvae, are difficult to study but may have dominant importance for establishment of relations between weather and population size.

Development of Immature Stages

Immature development is primarily a function of temperature and laboratory measurements may be reasonably applicable to field environments. Effects of temperature on development times of immature stable flies have been measured in several studies. Even in homogeneous larval media, the development times are quite variable and the minimum times appear more predictable than the average times for several individuals (Larsen and Thomsen 1940, Berry et al. 1976). The minima, the means and the standard deviations of intrastage development times appear to have fixed ratios to the minimum total development time over a wide range of temperatures, so that a simple model can estimate the distributions of time spent within a given stage (Berry et al. 1977). In field applications, temperatures within preferred larval habitats may need more study; the ability of larvae to move to warmer media during the winter (Berry et al. 1978)indicates that similar forms of thermoregulation may occur throughout the year.

Survival of Immature Stages

This component may be greatly affected by weather and biotic variables, thereby accounting for much of the short-term variation in populations. Direct field measurements of immature survival are so sparse that existing models have equated estimates of egg production, adult emergence and generation increase to provide indirect and average estimates. Direct measurements by Smith et al. (1983) were averaged over the summer. Direct measurements of pupal parasitization have indicated the magnitude of this mortality factor (Petersen and Meyer 1983). Hopefully, frequent, periodic and absolute measurements of egg production and adult emergence for extended periods can provide better estimates of weather effects on immature survival.

Development of Adults

Age classification by ovarian development not only provides a valuable ecological method, it is also directly related to egg production rates and provides additional framework for models. Nulliparous females can be readily classified by dissection into at least six age classes (Scholl 1980). Uniparous females can be sorted into at least three age classes. Berry and Kunz (1978) established relations for the effects of temperature on developmental rates of nulliparous females and average oviposition rates of parous females, but more detailed information is needed. Current data indicate that parous females produce 80 or more eggs every two days at 25 C.

Mortality of Adults

A simple model for adult mortality was proposed by Berry and Kunz (1977). Age-dependent mortality in the laboratory was so low that it can probably be neglected in the field, where other causes likely dominate. LaBrecque and Weidhaas (1975) estimated that adult mortality was 25.3 to 27.3% per day in outdoor cages. Unpublished data from the Livestock Insects Research Unit indicate that mortality at Nebraska feedlots is 17% per day or less. These estimates were based on the reasonable assumption that the lifetimes of stable flies are exponentially distributed, although rain or extreme weather conditions may cause unusual mortality for brief periods. Also, mortality may vary from the average because of certain activities, such as ovipositing.

Transition Events

Very limited data indicate that certain interstage transitions do not occur at temperature extremes which otherwise permit intrastage development. These extremes may only delay such transitions as ovipositing, but may cause higher mortality during egg hatch, molting, or pupation. Until more detailed data are available, transitional mortalities must be lumped together with intrastage mortalities.

Feeding, Reproduction and Other Activities

The ecological factors listed as activities in Table 1 have generally not been quantitatively described in field populatons. Nevertheless, observation of these behaviors has provided much of the existing knowledge of stable fly population dynamics. For example, visual counting of feeding flies on cattle has been and remains the major method for evaluating natural populations around cattle. Because feeding behavior of stable flies almost entirely determines the economic impact of the species, a quantitative estimate of feeding should be one major output of a practical population model. Therefore, the remainder of this paper will address the development of a submodel to describe feeding behavior.

A Submodel of Stable Fly Feeding Activity

Experimental Methods

Hourly counts of feeding (or resting) stable flies on the front legs of feedlot cattle were made through 16 summer days in eastern Nebraska. Concurrently with the counts, temperatures, humidities, radiation and wind velocities were measured at the periphery of the same lots. The experimental data were analyzed by an extensive series of stepwise regression procedures, which ultimately yielded the concepts and structure for a proposed model of feeding activity.

Experimental Results

For typical summer days in eastern Nebraska, the feeding patterns were consistently unimodal, with the daily peaks occurring between 13:00 and 16:30 hr (CST). The leg counts in ratio to the daily cumulative leg (or daily integral) leg counts are shown in figure 1. The daily feeding patterns are described by the equation:

$$\text{Ln}(Lc/Lcdc) = -10.074 + 1.1373\ t - 0.040781\ t^2 \quad [1]$$

where:

t = time of day, hr (CST),
Lc = avg. front leg count on 20 animals,
Lcdc = numerical integral of Lc for the entire day,
Ln = Naperian logarithm,
and
R = 0.8835, total correlation coefficient.

As an approximation, the value of R squared, 0.78, indicates that the precision of individual population measures can be improved by a factor of four by considering the time of day when leg counts are made. Also, Lcdc is proposed as a more general measure which is not affected by short-term variations in feeding activity.

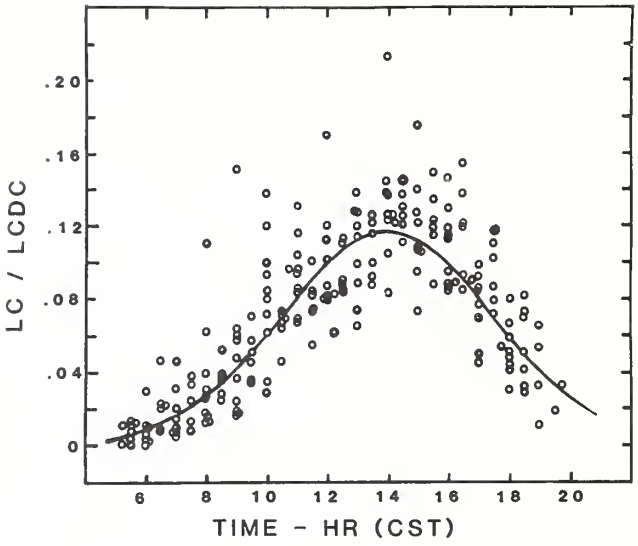

Figure 1. The ratio of leg counts to cumulative daily leg counts vs. time of day.

When weather terms were added to equation 1, no combination of weather factors predicted the ratio of Lc/Lcdc as well as the simple quadratic function of time. When the quadratic function of time was included with weather variables, the regression matrix appeared to be nearly singular. This result was credited to close correlations between temperature, radiation and humidity, which could all be related to time by various quadratic functions.

The intercorrelation problem was partially solved by recognizing that the unimodal feeding patterns were determined by the product of two separate factors, increasing appetite and decreasing numbers of unfed flies through the day. The factors were separated by expressing feeding rates in ratio to the partial cumulative of feeding rates for the remainder of the day. This quantity provided a measure of appetite, or feeding stimulus, which appeared to be adequately predicted by a linear function of time.

$$\text{Ln}(h) = \text{Ln}(Lc/(Lcdc-Lcc)) = -6.602 + 0.3775\ t \quad [2]$$

where:

h = feeding function, or appetite,
Lcc = cumulative of front leg counts until t,
and
R = 0.9445, total correlation coefficient.

Weather factors could be added to this equation without signs of singularity. Through stepwise regression procedures, coefficients in table 2 were selected as measures of responses in feeding to weather. Temperature was the most important weather variable and its effect was consistently described by a quadratic function. The predicted response was a maximum of 27.6 C when other weather factors were deleted from the equation, and 33.2 C when they were included. The correlations of both RH and radiation with temperature caused the shift in the relative

temperature response. Both RH and radiation varied with temperature to reduce responses at the higher temperatures and increase them at the lower temperatures. RH and radiation interacted with wind velocity so that relative responses were decreased by any changes of those factors that would increase drying rates.

A Model of Feeding Behavior

These experimental results allow a model of feeding behavior to be partially defined. The feeding function, h, is directly analogous to a hazard function for survival distributions (Gross and Clark 1975) and the exponential form of equation 2 corresponds uniquely to a least-extreme-value distribution for feeding times.

Table 2. Coefficients and relative responses of regression equations of effects of weather on Ln(h).

Factor	Equation A	Equation B
	Coefficients:[1/,2/]	
Temperature	0.6534	0.8310
Temp. squared	-.009137	-.01250
Radiation	-	-1.5188
Wind	-	-.1492
Radiation x wind	-	.07836
Wind x RH	-	.00159
Tot. correlation	.9768	.9872
	Relative Responses:[3/]	
Temperature for:		
100% max.	27.6	33.2
50% max.	18.9	25.8
10% max.	11.7	19.7
RH	-	.3435
Radiation	-	-.1038
Wind	-	.0051

1/ All coefficients are significant at error probability <0.01.

2/ Means of temperature, RH, radiation and wind for 1982 regression data were 26.77 C, 67.65%, 0.5376 KJ/m2/s and 14.44 Km/h, respectively. Standard deviations were 3.777, 14.93, 0.2679 and 6.551, respectively.

3/ For RH, radiation and wind, relative responses are fractional rates of change per standard deviation of the specified variable with other variables at their mean levels.

This distribution can be directly substituted for equation 1 to describe the data in figure 1. For a constant environment, figure 2 shows the relations between h (a measure of feeding stimulus), S (the unfed proportion of the population) and f (the least-extreme-value distribution). As the feeding function increases exponentially through the day, the unfed proportion of the population approaches zero asymptotically, so that the product of those terms describes the unimodal feeding patterns observed in Nebraska summers. The importance of this relation is that both S and f are entirely determined by h, the feeding stimulus. By modifying the function for h, almost any observed daily feeding pattern can be simulated. Thus the problems of measuring and simulating the effects of weather on feeding activity reduce to the problem of describing the responses of h. Fortunately, the feeding of most flies during this study seemed synchronized, with one engorgement per day, so that h could realistically be estimated from the daily feeding patterns.

The total feeding stimulus, h, is logically composed of two elements, hunger and short-term behavioral responses. For this study, hunger was crudely represented by a linear function of time. In a more complete model, the effects of

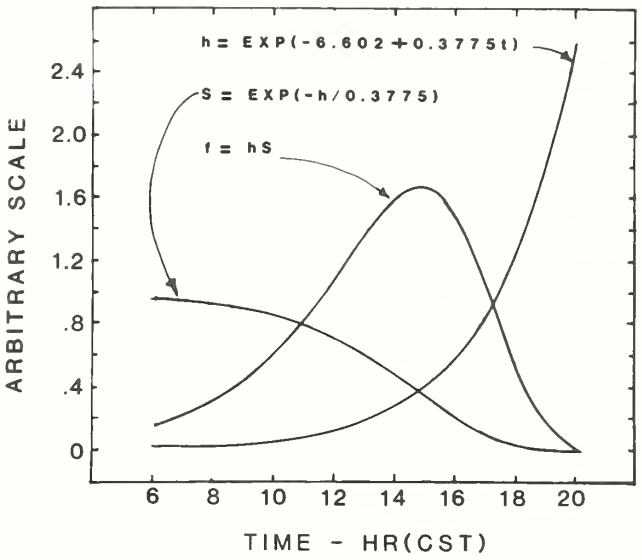

Figure 2. The total feeding stimulus (h), the proportion of unfed flies (s), and the feeding rate (f) vs. time of day.

temperature and other weather factors on the progressive digestion and metabolism of previous blood meals would be represented by an integral function of weather. The short-term behavioral responses to weather would be represented by regression equations similar to those in Table 2. In equation form, h would be:

$$h = \mathrm{EXP}\left(\int_0^T F(r)\,dr + G(T)\right) \qquad [3]$$

where:

T = time after previous engorgement,
r = dummy variable of integration,
F(t) = digestion and metabolism as a function of weather,

and
G(t) = behavioral responses as a function of weather.

By expressing h as an exponential function, the joint action of both elements is realistically simulated; the degree of hunger must reach a certain level and the immediate environment must be suitable for flight before h increases to indicate an increasing probability of feeding.

This proposed model has the flexibility to describe a wide a variety of observed feeding patterns. During this study, the stable flies seemed to feed once per day over a moderate range of summer conditions. Presumably, the amounts of ingested blood varied to maintain an adequate level of metabolism for those varying conditions. Bimodal feeding patterns at other locations can be readily simulated if midday conditions reduce the current feeding stimulus, or if cumulative daily temperatures are high enough to cause flies to feed twice daily. In the latter case, the model can be applied separately to different parts of the population. A similar procedure would be required when cooler conditions cause flies to feed at intervals of two or more days.

In summary, analyses of experimental data define a partial model of stable fly feeding behavior. As with most biological models, unexplained errors and incomplete data require additional experimentation. The incomplete model strongly indicates that relations between fasting time, the amounts of ingested blood and the environment need to be established. Also, better measurements of the feeding time required for engorgement would greatly improve our current ability to estimate population size.

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COMPUTER MODELING OF POPULATIONS OF THE HORN FLY[1/]

J. Allen Miller[2/]

INTRODUCTION

The horn fly, Haematobia irritans (L.), has been a serious pest of cattle in the United States since its introduction in about 1887 (Riley 1889, Smith 1889). Although the exact economic losses due to this pest are difficult to determine, it is estimated that horn flies cost the cattle industry $300-700 million/year (Anon. 1976, Drummond et al. 1981). Despite an impressive collection of weapons developed for horn fly control, ranging from insecticides to the release of sterile males, the horn fly continues to be a problem. The insecticidal ear tag, although a tremendous advance, has recently encountered a problem with horn fly resistance to the pyrethroid insecticides in the tag. It is becoming increasingly apparent that no single tool in itself is a panacea. Effective and efficient control will depend on our ability to integrate the use of these tools and our knowledge of the biology and ecology of the fly in the development of pest management strategies.

Development of a strategic approach to pest management requires a detailed knowledge of the population dynamics of the pest. An extensive literature deals with the life history and biology of the horn fly. McLintock and Depner (1954) and Bruce (1964) presented comprehensive reviews. Morgan and Thomas (1974) compiled an annotated bibliography of the horn fly including over 1100 references and a later supplement contained an additional 402 references. A brief outline of the life cycle of the horn fly is shown in figure 1.

Even if all the information relating to the population dynamics of the horn fly were known, there would still exist a need for a method of integrating this data into a system. The structuring of population models is one method of accomplishing this task. Because of the fragmentation of information and the difficulty of visualizing the overall horn fly production system, much of the information already known is not being used in making decisions as to control approaches.

On the basis of the preceding reasoning, we began efforts to structure a model and develop a computer simulation of the population dynamics of the horn fly. Our objectives were 3-fold:

1) to integrate existing information concerning the processes governing the total horn fly production system;

2) to provide a framework within which to structure more meaningful laboratory and field experiments relating to data needs;

3) to develop a computer simulation of the population dynamics of the horn fly.

My effort here will be to describe the basic structure of the model, how its various components are linked, and the assumptions involved. Assumptions necessitated by a lack of quantitative data point to specific research needs.

DESCRIPTION OF THE MODEL

The horn fly population is represented in a discrete, deterministic model. The emphasis in this description is on what the model accomplishes and what the assumptions involved are rather than on how these things are accomplished in the computer program. The population is divided into its distinct life stages of eggs, first, second, and third instar larvae, pupae, and adults. Each of these life stages is further divided into subclasses of 1 day of age intervals. A simplified schematic of this compartmentalization is shown in figure 2.

Each subclass cell represents the number of horn flies of a particular life stage which are of equal age. The number of horn flies in each stage can be obtained by summation of all subclasses for that stage. In like manner, the total population is a summation over all life stages for a particular day.

The particular structure used for the model was selected for its simplicity and versatility and facilitates the incorporation of new data which are being continually developed. This form of representation appears particularly suited to populations of the horn fly because of the horn fly's unstable age structure. Age-specific oviposition rates, survival rates, and development rates can be functions of both time and physiological age. Additionally, control strategies aimed at one or more life stages can be more easily evaluated within this structure.

In the model, the population on the current day is multiplied by the appropriate survival factor and moved forward to the next subclass. An accounting is maintained of the accumulated degree-days above the developmental threshold for individuals in each subclass. When these individuals have accumulated the appropriate number of degree-days, they are moved to the first subclass of the next life stage. The model is described in the order of events in the life cycle of the horn fly for a typical year.

Emergence From Diapause

The horn fly can be found on cattle throughout the year in the warmer climates of the United States (below 30° latitude). However, in most

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1/ Diptera: Muscidae.

2/ Research Agricultural Engineer, ARS-USDA, P.O. Box 232, Kerrville, TX 78029-0232.

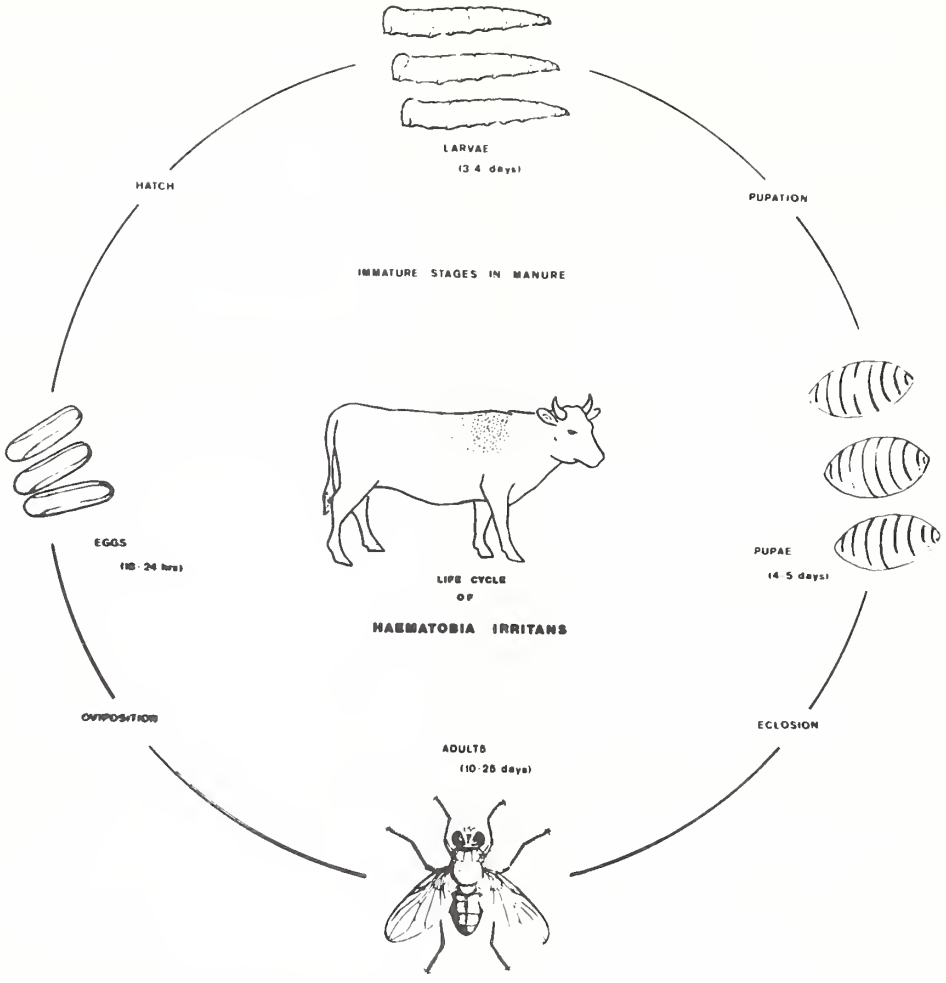

Fig. 1. Life cycle of the horn fly.

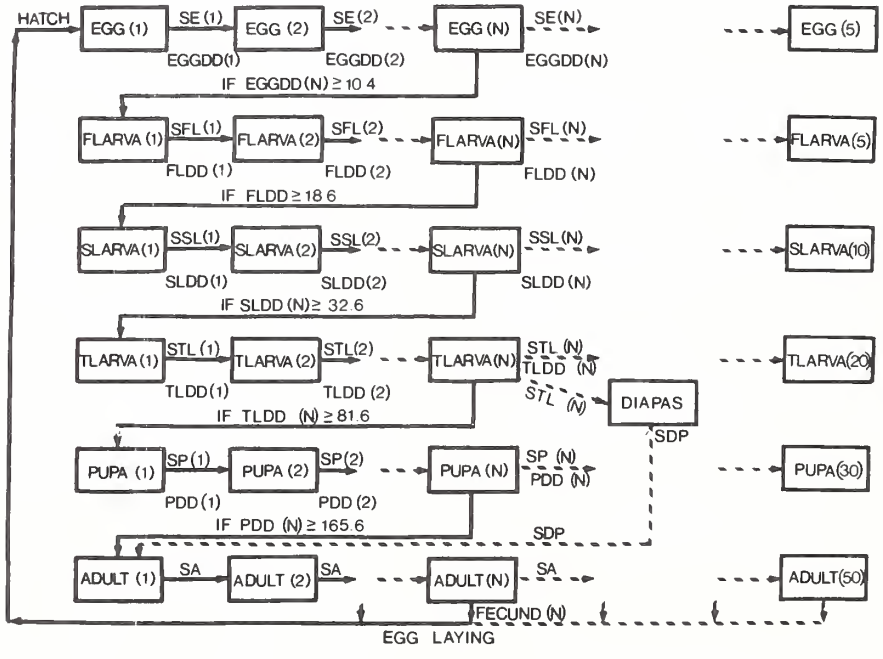

Fig. 2. Simplified schematic of the population simulation.

areas of the country, the fly overwinters as diapausing pupae. The entrance of the fly into the diapause state will be discussed later.

In northeast Mississippi (Hoelscher and Combs 1971a) and in north Texas (Bruce 1964), adults begin emergence from diapausing pupae about mid-March to mid-April. Presumably, emergence occurs earlier in warmer and later in cooler climates. Additional analysis of the data presented by Hoelscher and Combs (1971a) and Bruce (1964) indicates that peak emergence coincides with the first occurrence of a 14-day mean temperature greater than 18°C in the early part of the year. Additionally, the emergence appears to begin and end ca. 20 days prior to and after the peak. On the basis of these data, a triangular pattern of emergence was installed in the model such that the portion of pupae emerging from diapause increased linearly from 0% to 5% per day over the first 20 days and declined again to 0% over the last 20 days.

Survival Of Adults

In tests conducted during the summer months (June-September), 50% of newly emerged flies were found to survive 4.98 days (Miller, 1977) for a day-to-day survival of 87%. Krafsur and Ernst (1983) while studying the age composition of horn fly populations obtained an estimate of 86% probability of survival through 1 day. Because the adult fly is continually on cattle, except for the female leaving to oviposit on freshly dropped manure, temperature is expected to have only a small effect on adult survival. Flies tend to move to the underbelly of the cow during the peak temperature and solar radiation periods of the day and to the back in cooler periods. To reflect this movement, daily adult survival was assumed to increase linearly with a decreasing temperature from 84% (50% surviving to 4 days) at 38°C to 90.6% (50% surviving to 7 days) at 10°C. Below 10°C, flies become less active and, therefore, are expected to be more susceptible to mortality, as a result of the animals' defenses, such as tail switching and rubbing. Morgan (1964) theorized that at colder temperatures flies become immobile and unable to return to the host after being brushed off or leaving for deposition of eggs. Therefore, survival was made to decrease linearly below 10°C to total mortality at a mean air temperature of 0°C. Above 38°C, survival was also assumed to decline linearly from 84% to total mortality at 50°C. Therefore, adult survival is treated as having both an upper and lower temperature threshold.

Another aspect of adult survival considered in the model is that of density dependence. Increasing density was assumed to decrease the longevity of adults. As the population increases the available "safe" resting area on cattle decreases. Therefore, flies would be forced to move from the favored shoulder area where they are relatively safe from the tail switch and head of the animal to more "vulnerable" areas of the back and sides. In addition, crowding of flies on the cattle may force some flies to leave the current host in search of another and thereby decrease survival probability.

The density-dependent factor acting on adult survival was assumed to become effective as the population exceeded 250 flies/animal. The normal adult survival as computed by the temperature function previously discussed is multiplied by the density-dependent function [1.125/(1+.0005 *No. of flies)] to determine a new survival rate.

Oviposition And Hatch

Little quantitative information is available on egg-laying habits of the horn fly. Bruce (1964) reported that eggs developed in the female fly in batches of 24 and that about 15 batches were produced during her lifetime. However, the largest number Bruce observed to be deposited at any one time was 14 eggs. Schmidt and Blume (1973) found an average of 19 ovarioles/female but observed a decline in the number of functional ovarioles with increasing age. Schmidt et al. (1972)[1/] also demonstrated a decline in eggs laid per female from a maximum of 15 to 17 on the fifth day of age to two to three on the 25th day of age under laboratory conditions. A summation of the eggs per female over the 20 days indicated a total of ca. 125 eggs/female.

Kunz and Cunningham (1977) reported that gravid females from a field population laid an average of 18.6 eggs/fly in the first 24 h of laboratory confinement. They also noted no appreciable change in the number of eggs per gravid female over the March-November observation period. From the field collections, they observed only 34-46% of the females were gravid, indicating an average of less than nine eggs/day per female in the population.

Until more quantitative data become available, it has been assumed that a single female will lay a maximum of 200 eggs in a lifetime and that these eggs would be distributed over a 25-day period with a linear decline from a maximum of 16 eggs on the first day of egg laying to no eggs on the 25th day. Palmer (1979) reported data on caged flies in a laboratory environment which support this assumption.

Additionally, the age at which oviposition begins was made temperature dependent. Egg-laying was assumed to begin on the fourth day of age for temperatures greater than or equal to 25°C, and the period until first oviposition to increase linearly to a maximum of the 10th day of age for 10°C.

1/ Unpublished data.

The hatch of eggs was assumed to be a constant 95% for all temperatures above 10°C (Bruce 1964, Thomas and Morgan 1972). Bruce (1964) reported that the viability of eggs was unaffected by exposure to a temperature of 9°C for 24 h. Assuming that the longer incubation period at cooler temperatures increases both the probability of mortality due to predation and desiccation, hatch was decreased linearly from 95% at 10°C to 0% at 0°C. Additionally, the occurrence of a minimum temperature of 0°C or less was assumed to kill all eggs not yet hatched.

Rate Of Development Of Immature Stages

The model incorporates the temperature-dependent rate of development function described by Miller (1977). The progression from one life stage to the next is dependent on the accumulation of a minimum number of degree-days above a threshold temperature of 11.16°C. In summary, eggs hatch upon the accumulation of 10.4°C-days, first-instar larvae molt to the second instar when 18.6°C-days have been accumulated, second-instar larvae go to the third instar at 32.6°C-days, third-instar larvae pupate when 81.6°C-days have accumulated, and pupae eclose at 165.6°C-days (fig. 2). The data upon which these figures are based was collected over the range of mean-air temperatures of 16°C-28°C. Within this range, the assumed linear relationship between rate of development and temperature produced a highly significant regression ($P < 0.01$). However, the derived relationship could not be used with confidence for temperatures outside the range of the observed data (16°C-28°C). Rate of development usually greatly exceeds the predicted rate, as the temperature approaches or drops below the theoretical threshold of development (Andrewartha and Birch 1954). In order to simulate the accelerated rate of development at the lower temperatures (016°C), a simple linear relationship was assumed between degree-days and temperature. In this manner, the maximum development time from egg to adult becomes 70 days at 0°C and equivalent to the number of cells allocated to the immature stages in the model (fig. 2). In cases below 10°C, development time becomes an academic consideration since our studies have shown that eggs and first larvae are killed at these temperatures.

An accounting of accumulated degree-days is maintained for each age group of immature insects to enable transitions to the various stages in the model.

Although other development-rate models are available (Berry et al. 1977, Sharpe and DeMichele 1977) and offer specific advantages, none of these have yet been tried in our model. Palmer et al. (1981) used such a model for horn fly development; however, their model was based on a laboratory study where the temperature of the rearing media was equal to that of the surrounding air temperature. Under field conditions, the temperature of the manure containing horn fly larvae cannot be expected to equal air temperature due to the interface of the dropping with the soil and to the effect of solar radiation.

Survival Of The Immature Stages

Perhaps the most difficult component of the model is that of survival of the immature stages in the manure droppings. Kunz et al. (1970, 1972) reported an average of 6.6 flies/dropping for those fully exposed to competition and predation. Thomas and Morgan (1972) found the average horn fly mortality from egg to adult for each of 3 years in Missouri to range from 92.6 to 97.7%. In neither case were these observations related to environmental conditions.

For the model, a relationship developed by Miller (1977) which relates survival to three environmental variables, rainfall, mean daily low and high temperature was used. This relationship was developed by use of the stepwise regression of 14 variables on observed survival. Although not an ideal description, it is the only one available.

The total survival of the immature stages from egg to adult was then equally apportioned to each day of the total development time. Although daily survival is expected to be greater for the third-instar larvae and pupae (Thomas and Morgan 1972), until more quantitative data are available, the assumption of equal daily survival for all stages should suffice.

The onset of cold weather produces exceptions to the described method of calculating survival of immature stages. The occurrence of a minimum temperature of 0°C was assumed to kill all eggs, first-, second-, and third-instar larvae. Additionally, 50% of the pupae not in the diapause state were assumed killed by an overnight low of 0°C.

Entering Diapause

Numerous researchers have studied factors influencing the onset of diapause in the horn fly (Larsen and Thomsen 1941, Hammer 1942, McLintock and Depner 1954, Bruce 1964, Depner 1961, 1962, Hoelscher et al. 1967, Wright 1970, Hoelscher and Combs 1971a). Diapause has been found to be facultative, induced by factors associated with the simultaneous decline of day-length and temperature. At Camp Stanley, TX Kunz et al. (1972) reported that all emergence from eggs laid in November occurred the following spring. Furthermore, they detected no flies emerging from droppings deposited in December and January. Confirming results were obtained in later studies (Kunz and Cunningham 1977). Hoelscher and Combs (1971a) found that October was the principal time for development of diapausing individuals. From their data which provided both date, temperature, and percentage of horn flies entering diapause, a generalized relationship was formulated for use

in the model. It was assumed that diapause begins in the fall of the year (decreasing day-length) when the 2-week average temperature reached 20°C. The percentage entering diapause was made a linear function of time with a gradual increase in number of third-instar larvae which eventually pupate and enter diapause. The percentage entering diapause was made to increase from 0% at the onset of diapause to 95% 50 days thereafter. Ideally with improved data, diapause could be better defined only in terms of decreasing temperature and photoperiod. The fact that adult horn flies can be found in low numbers even in December and January in College Station and Camp Stanley, TX supports the assumption that <100% of the flies diapause; a few must progress directly through to the adult stage.

No data were available to determine the portion of diapausing pupae which survive to emerge the following spring. Therefore, 20% were assumed to survive through the diapause state.

SIMULATIONS

The described model was incorporated into a computer program for simulation of horn fly populations. Daily temperature and rainfall data for the years 1973 and 1974, as obtained from the National Climatic Center records for College Station, TX were used. These data were used because of availability of corresponding data on field populations of horn flies for these years. Each simulation included a 365-day year and began with a starter population of 5000 pupae in diapause on January 1.

Although the program generates an estimated number of insects at 1-day intervals for each life stage, only the output of adult horn fly estimates is used because it is the only stage for which field data enables verification.

Figures 3 and 4 present the results of simulations of horn fly populations using the 1973 and 1974 weather data, respectively. In addition, observed field populations in the College Station area, as reported by Kunz and Cunningham (1977), are presented for comparison with the simulation. The field populations are from one herd of 95 Hereford cows and calves.

A study of figures 3 and 4 indicates that the simulation follows the seasonal variations of horn fly populations. The simulated and the observed populations both indicated a spring build-up with a peak population in April-May followed by a decline during mid-summer. A population increase began in late summer and produced a second peak in October-November. The simulation for both years began with a starter population of 5000 pupae in diapause. The simulated populations for 1973 ended with 5861 pupae in diapause, whereas, 4429 pupae were in diapause at the end of the 1974 simulation. In general the simulation appeared to mimic the changes in field populations in response to weather factors, such as rainfall and temperature.

However, the simulated results are at variance with observed field populations with respect to several details. The simulation estimates of fly populations are not in precise agreement with the field estimates of population levels. Additionally, the exact date of population peaks does not coincide for the two population estimates. For example, it is interesting to note that the spring peak for the 1973 simulation preceeds the observed field population peak but lags the field population during the fall whereas, the reverse occurs in the 1974 simulation. A comparison of weather for these 2 years indicated important differences. The mean annual temperature for 1973 was 19.3°C as compared to 19.7°C for 1974. The last spring minimum and the first fall minimum of 0°C or less occurred April 10 and December 17, respectively, during 1973. Whereas for 1974, these minimums occurred February 26 and November 29. The total rainfall during 1973 (151 cm) exceeded the rainfall for 1974 (127 cm). Although rainfall during most months of 1974 was below normal, August, September, October, and November had exceptionally high rainfall.

The variation of temperature and rainfall between years and the distribution within a year point to the need to consider when these factors become critical to survival of immature stages of the horn fly. If moisture is ample to meet basic developmental requirements, growth of the population may be limited by one or more other factors which are less available. In an exceptionally dry period, moisture may become the most important limiting factor. Therefore, ideally a description of immature survival of the horn fly should incorporate a limiting factors concept.

Several points are worthy of consideration with respect to apparent discrepancies between simulated and observed populations. The estimate of field survival of immature stages of the horn fly considers only rainfall, temperature, and interspecific competition and predation. Miller (1977) indicated that these factors could account for ca. 75 percent of the observed variation in survival. Furthermore, interspecific competition and predation was only an indicator variable; therefore, changes in level of competition and predation which might be expected to vary with seasonal changes were not considered.

Additionally, the observed field populations are in themselves merely estimates. Generally, the observer approaches a herd of cattle and with the aid of binoculars attempts to estimate the number of horn flies on each of 5-10 animals. From these estimates, an average population is determined. Although a degree of skill can be developed in this art, the accuracy of the technique has not been confirmed. It is not unusual for two skilled observers to be 100-200 flies different in their estimates, particularly when populations are large (>500/cow). Also, observations on several herds over a broader area should be more representative of field populations than observations on a single herd at one location. For example, Kunz and

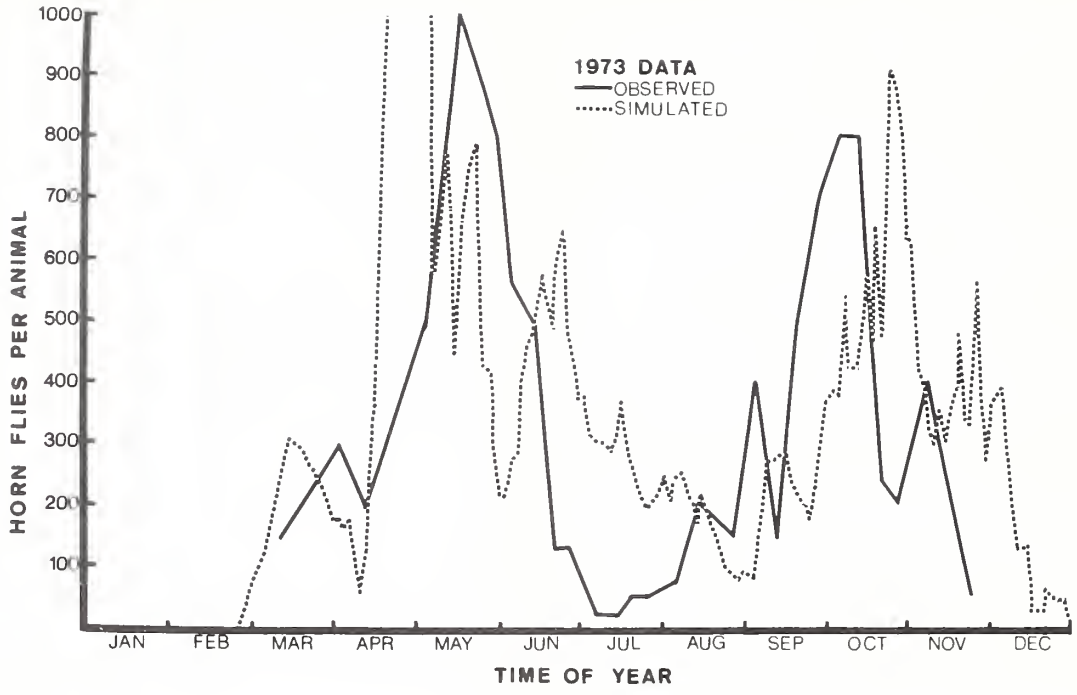

Fig. 3. Simulated and observed horn fly populations, 1973, College Station area.

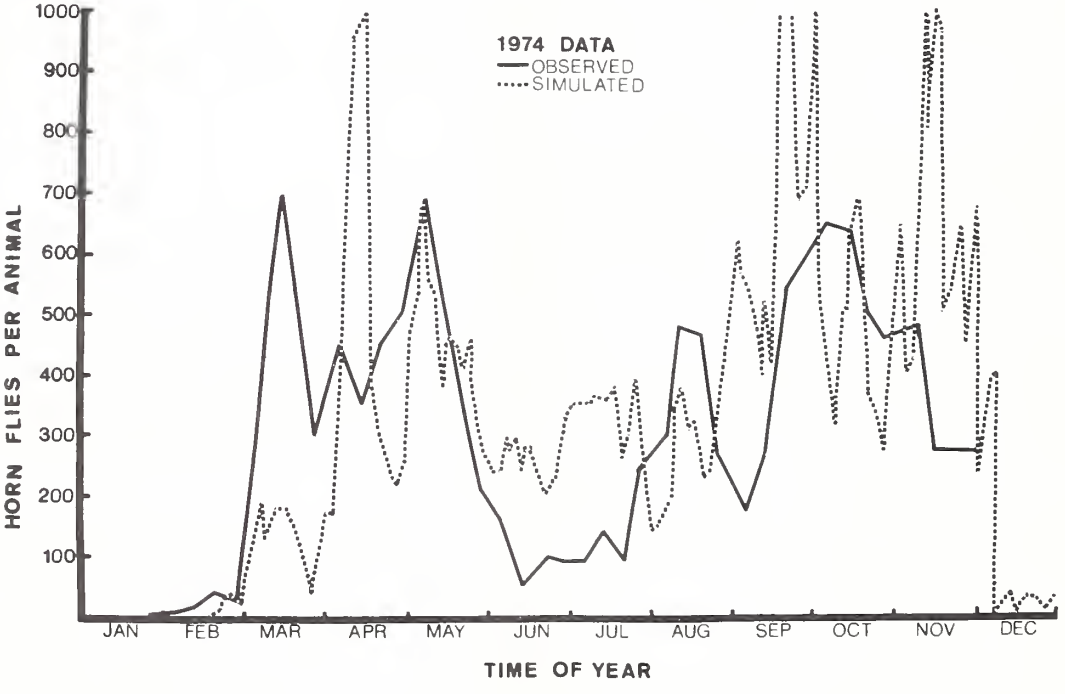

Fig. 4. Simulated and observed horn fly populations, 1974, College Station area.

Cunningham (1977) point out that the mid-summer declines observed in 1973 and 1974 on the Caldwell herd were more pronounced than those previously observed on other herds in the area. Therefore, differences in simulated values and observed populations cannot be totally attributed to the weakness of the computer simulation.

CONCLUSIONS

Despite its limitations, the described simulation model will be useful as an aid to the evaluation of control strategies for long-term effect against horn fly populations in an area. A proposed control or combination of controls can be simulated on the computer model, and the results evaluated as to potential effectiveness and efficiency. Those strategies appearing most promising from the results of the simulation can then be investigated under field conditions.

Additionally, the simulation model has served as a framework within which to more efficiently study horn fly population dynamics. Many areas needing attention have been identified, and a focus of attention in these areas has served to unify research on the horn fly. Recent efforts have been made to add to our database. Studies to determine age-specific fecundity and to obtain data relative to entrance into, survival during, and emergence from diapause are nearing completion. At the moment, the model is serving us best by guiding our research. Refinement of the system simulation resulting from new and improved data will further increase the utility of the simulation as an aid to the decision-making process in developing improved horn fly control.

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A MODELING SYSTEM FOR HORN FLIES ON CATTLE

W. O. Haufe[1]

Computer simulation, laboratory experiments, epidemiological studies, field correlations and tests of pest management practices on a large ranch were combined in a 12-year program to develop a modeling system for the dynamics of the "parasitic population" of horn flies on cattle. A conceptual interpretation of host-parasite relations governing the basic functions of the model have been fully assessed and verified. These relations have been integrated in a master model of the host-parasite system to serve as the framework for more detailed analyses and sub-modeling of various components of pest management and cattle production. A protracted development of the modeling system was designed primarily to establish the hierarchy of a number of interacting biological processes within an ecological approach to parasitism.

Functional modeling and simulation of the dynamics of parasitic populations of horn flies on cattle involves at least three biological systems operating in the host. Cattle respond to parasitic flies through the neurosensory system, the immunochemical system, and a syndrome of social behavior that operates for the collective protection of animals in an open environment. The three systems operate simultaneously and, therefore, pose considerable complexity in a quantitative analysis of host-parasite relations.

The behavioral syndrome has been found in extensive studies to be the overriding system for any simulation of host-parasite relations for animals exposed to flies on pasture and native range. Consequently, it determines the form of a functional master model which has been assessed to accommodate more specific sub-models for physiological processes such as adaptation, immunosensitization, and resistance of animals in the host-parasite system.

The Model

The master model for a parasitic population of flies represents the cumulative numbers of parasites in the prevalence or growth of an infestation (G_i) with time. It conforms with a logarithmic decay function in which

$$G_i = N_1 - f(x) = N_2 C^x$$

and

N_1 = number of parasite burdens or hosts observed,
N_2 = the size of the population of host samples,
$f(x)$ = frequency with which the infestation remains within a given limit,
C = a quantitative measure or index of host tolerance to parasites for the unit of host population being observed,
x = number of parasites.

Parasite sampling and other measurements in the model are concerned with change (dynamics) in rate of infestation (disinfestation) and distribution (redistribution) of pest burdens among animals. These dynamics are related to time in the course of an infestation cycle. The model serves to express changes in the statistical distribution of the parasite population in terms of physiological and behavioral function in the social organization of the host population.

The important biological function simulated by the model is a process of host-parasite metastasis. Host-parasite metastasis corresponds with the established medical definition of the term as applied to infectious disease. It defines a state of continuous dispersion of an infestation or infection of parasites among individual animals away from the focus of parasitism in a social unit or population of hosts. Host-parasite metastasis is a continuing process throughout the course of an infestation and leads to a stable distribution of parasites when hosts are exposed to a constant or tolerable density of parasites. It has the significant function of sustaining a state of host-parasite regulation in the face of increasing or varying rates of infestation with time. Therefore the model in graphic form "behaves" according to the mediation of interacting behavioral and physiological systems in the host to display the state of the host-parasite system.

Stability, as a result of a steady influence of host-parasite regulation in the course of infestation, is expressed as a rectilinear relation for distribution of the parasite burdens according to the model (fig. 1-a). Excessive exposure to an increasing density of parasites leads to a typical aberration in parasite distributions corresponding to figure 1-b. Rapid disinfestation or collapse of infesting populations of parasites displays an opposed aberration (fig. 1-c).

If host-parasite regulation is sustained successfully by metastasis throughout the complete course of an infestation cycle, then the model displays a series of rectilinear regressions for parasite distributions to accommodate an increasing parasite burden on the social unit of hosts (fig. 2). The range in numbers of parasites per host increases, but an exponential distribution of the parasite burden is sustained by continuous dispersion among hosts. Under epidemiological conditions common to southern Alberta, this stability in host-parasite regulation is maintained consistently at moderately increasing fly burdens in which the mean for the social unit remains below 230 flies/animal.

If rates of infestation increase rapidly and exceed an average of 230 flies/animal in the course of an infestation, the host population

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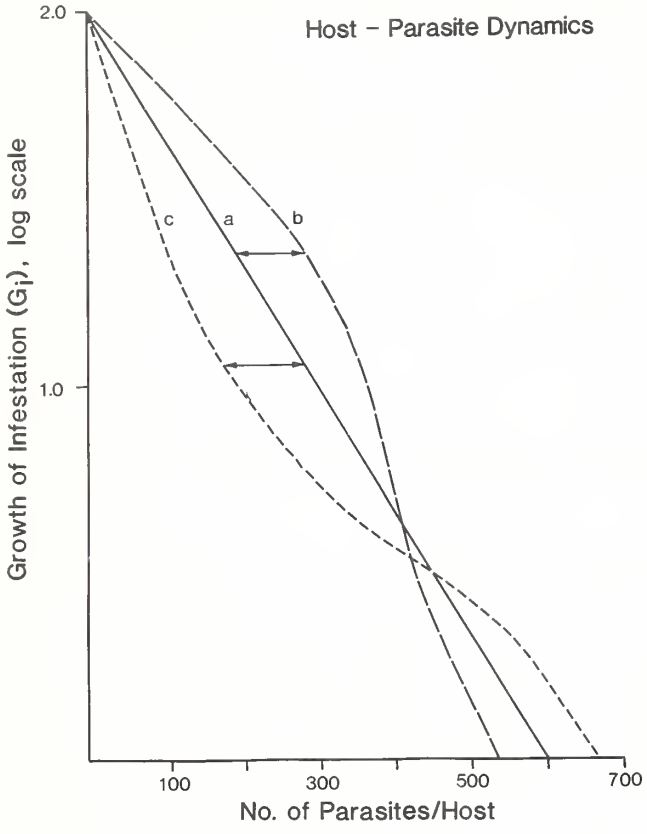

Fig. 1. Distribution of the parasitic population of horn flies among bovine hosts mediated by host-parasite metastasis.

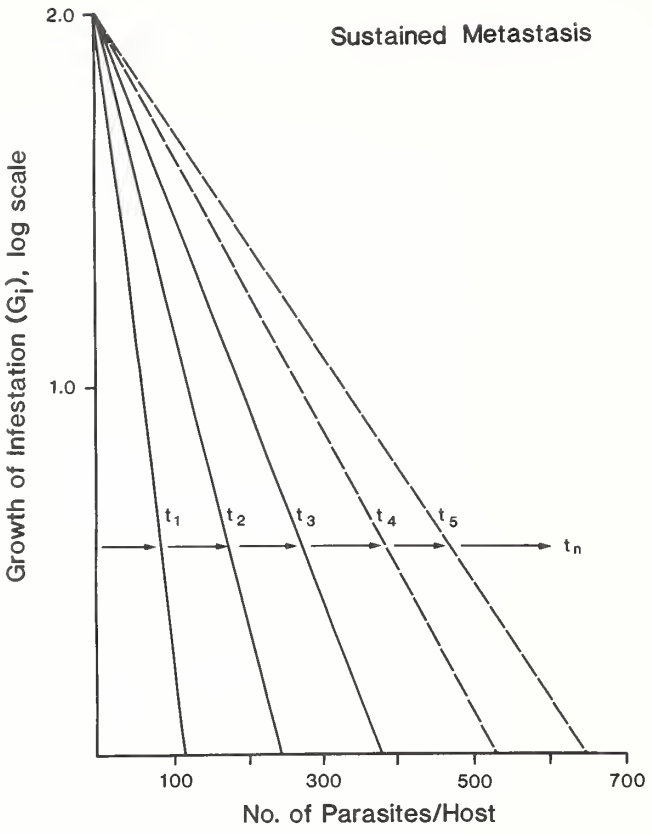

Fig. 2. Stable distribution of the parasitic population of horn flies among bovine hosts during host-parasite regulation of increasing abundance during an infestation cycle.

fails to maintain host-parasite metastasis. Under excessive exposures to flies, such as during a severe outbreak, the model displays a series of regressions in time for G_i with increasing deviation from the stabilizing exponential distribution (fig. 3). Metastasis may not be established in a sudden or severe outbreak until the course of the infestation has passed its peak and is in continuing decline.

Experimental Demonstration of the Model

In contrast with a statistical or correlative model, a functional model must be open to experimental verification of the system. This experimental verification was designed on a permanent irrigable levelled pasture developed to maintain grazing animals continuously throughout the course of a complete infestation cycle of horn flies. Two fenced fields of equal shape and area and drained along a common boundary were established with cultivated grasses, each sufficient to support 20 cattle without spelling during the summer (fig. 4).

Animals were selected for uniformity in two stages to compose experimental social units. A group of 70 yearling heifers was selected in late winter for uniformity in breed, colour, age, body weight and body conformation for a performance test in a feedlot to be completed before the emergence of horn flies in spring. Forty of the original 70 animals were selected further for uniformity in growth rate over a six-week period in the performance test. Following the performance test, 20 of the uniform animals were assigned by chance from pairs established by growth performance to each of the two fields before the first emergence of post-diapausing flies. One of the groups was designated for selection as a subherd with high tolerance to natural exposure to horn flies, the other for selection of low tolerance. The subherds were rotated between pastures on Monday, Wednesday, and Friday of each week to equalize environmental influence, variation in pasture, and exposure to a common population and course of infestation of horn flies.

Horn flies were counted on individual animals in early morning immediately before each rotation of the sub-herds. Animals in each sub-herd were ranked for tolerance of flies, TH_{1-20} for the high tolerance selection, TL_{1-20} for the low tolerance selection. Animal TH_1 transferred to sub-herd TL and animal TL_{20} to sub-herd TH. This procedure forced each of the sub-herds to re-establish host-parasite metastasis at pre-determined intervals of time, one for a higher

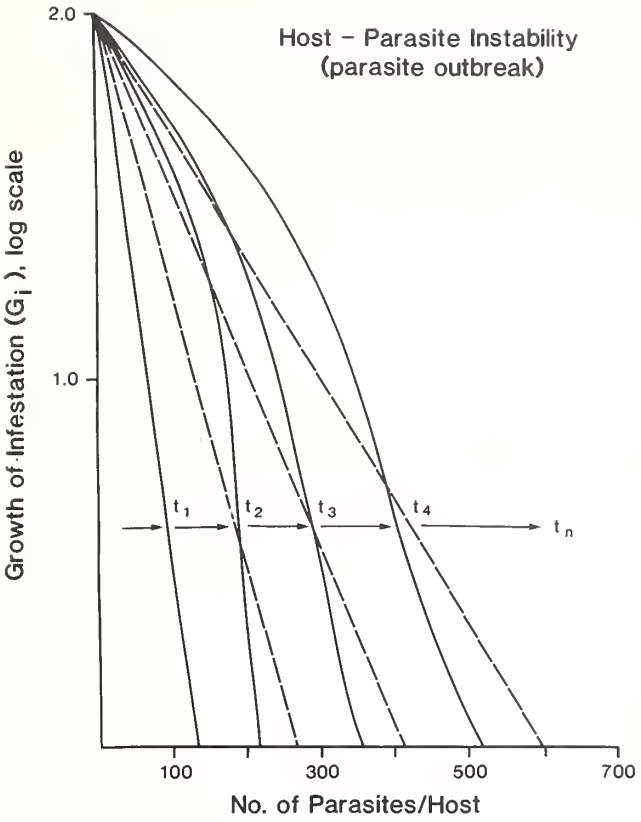

Fig. 3. Unstable distribution of the parasitic population of horn flies among bovine hosts during increasing abundance in an infestation cycle exceeding the host-parasite regulatory level.

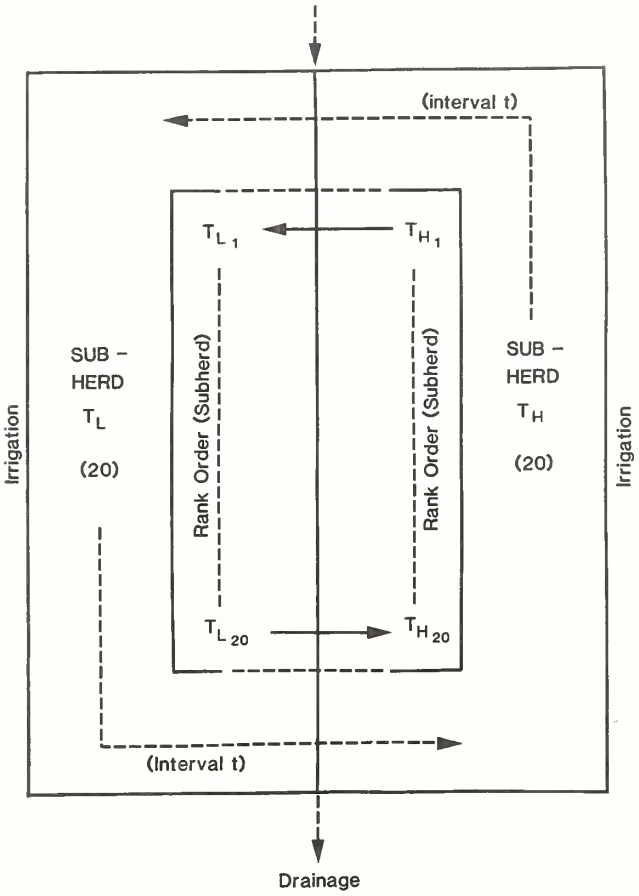

Fig. 4. Schematic diagram of the design of a laboratory-pasture experiment to demonstrate host-parasite interactions in a host-parasite regulatory system.

and one for a lower level of selection for tolerance of flies in response to a common level of exposure to reproducing and invading parasitic populations. A system of regular reciprocal transfer of animals TH_1 and TL_{20} in conjunction with regular rotation of sub-herds facilitated various measurements for the dynamic interaction of behavioral and physiological processes that influence the host-parasite system. Use of the model to analyze and to quantify various responses of cattle to horn flies is presently being elaborated in a number of other manuscripts for publication.

Operation of the Model for Host-Parasite Analyses

The model is operated conveniently for analyses in computer programming of host-parasite relations as a logarithmic transformation of the form:

$$\log_{10} [N_1 - f(x)] = \log_{10} N_2 - x \log_{10} C$$

Data from field studies at Lethbridge are routinely analysed in a time interval of 1 week. One program provides a plot of the cumulative numbers of parasites or growth of an infestation (G_i) for the weekly period. Another provides a plot of the cumulative numbers of parasites or growth of an infestation for the total period elapsed in the course of the cycle of infestation. The first indicates the state of metastasis for infestation at a given point of exposure to flies. The second displays the capacity of host animals as a social unit to maintain a system of host-parasite regulation during the course of a complete cycle of infestation.

Applications

The host-parasite model simulates a distribution of the parasitic population of horn flies among cattle in response to behavioral and physiological processes employed by the host to regulate or resist the infestation. It defines the state of the host-parasite system in relation to combined processes of infection at any prescribed time interval in the course of an infestation cycle. Therefore, it displays the function of the host-parasite system as well as the numerical distribution of the parasitic population.

As a simulator of the host-parasite system, the model is a tool for research and management of the 'parasitic' population of horn flies. In conjunction with appropriate experimental design, it is being used in research to identify and to quantify the parameters of host-parasite interaction. Such parameters include physiological resistance, tolerance, and susceptibility in hosts to natural infection, neurosensory and immunosensory response to parasites under field conditions, epidemiology and parasite dispersal within grazing areas, and physiological adaptation to parasitism in host populations. The model provides a means of integrating and quantifying these parameters of host-parasite interaction, especially those defined in controlled experiments, as an ecological impact in the host-parasite system under natural field conditions.

The model is a useful tool in defining the effectiveness of pest control practices within essential ecological considerations of fly dispersal and host behavior. It simulates the overriding ecological conditions for bioeconomic assessments of the benefits to be expected from pest control in management of cattle on pasture and range. Its simulation of host-parasite regulation as an ecological condition of animal production has an advantage in interpreting the real quantitative benefits from tactics and strategies of pest control in operational management systems.

Future Research

The present design of the model defines the distribution of the 'parasitic' population of horn flies among individual hosts within the grazing range of a herd or population of cattle. It is primarily a model of host-parasite function and determines the state of parasitism at the population level for a given seasonal cycle of infestation. Prediction of abundance of flies contributing to a cycle of infestation depends on a model of the 'reproducing' population relative to parameters in the environment of permanent grazing areas. Future research will be required to develop a life table for horn flies with appropriate coupling of the 'reproducing' and 'parasitic' populations. A combination of these models is needed to estimate seasonal generation of horn flies in pastures in relation to parasitic burdens and the range of grazing animals. Such a combination could complete a modeling and simulation system as a tool for all purposes in pest management.

A MODEL WHICH RELATES CAPTURES AND POPULATION OF FACE FLIES TO WEATHER IN MARYLAND

L. G. Pickens[1]/ and D. K. Hayes[2]/

Abstract

A model which calculated the expected 9-day moving averages of catches of adult female flies, Musca autumnalis De Geer, and which was derived from data obtained in 1978, 1979 and 1980, gave calculated catches which approximated the actual catches on standard pyramid traps in Maryland pastures in 1981 and 1983. Catch sizes were influenced by temperature, rainfall and size of the initial population.

Since relatively little is known about the population dynamics of face flies, Musca autumnalis De Geer, under field conditions (Pickens and Miller 1980) and since our sticky trap captures of face flies over 4 years provided us with 3-day catches over the entire fly seasons (Miller et al. 1984), we attempted to develop a mathematical model which would give calculated female catch values which are correlated with the dates and relative sizes of the actual catch values and which was based on field air temperatures and rainfall. The resulting model reported here is only intended to enable the researcher to calculate probable female catch sizes and the dates of adult emergence for each generation of flies under field conditions in Maryland. It is only assumed to be true for estimates based on fly catches and weather records obtained under the conditions of our tests.

MATERIALS AND METHODS

Field Data

Three white, sticky, pyramidal traps (Pickens et al. 1977) were placed in each of four beef or dairy farm pastures in Howard County, Md., in 1978, 1979, 1980, 1981 and 1983. At 3 day intervals between March 1 and October 1 in 1978 1979, 1980 and 1981 and between June 1 and September 1 in 1983, the sticky trap coverings were replaced and the numbers of captured female face flies were recorded. The traps were placed about 100 m apart at sites near cattle trails, streams and forest edges (class 1 and 2 trap sites, Pickens and Nafus 1981). The pastures contained hills, broad lowlands, a swamp, streams, and numerous trees. Between 25 to 40 cows, calves and one bull were in each pasture each year.

Mathematical Treatment of Data

The catches from the three traps at each farm were averaged at each collection date to obtain a mean one-trap catch per 3-day period and then the mean 3-day period catches before, on, and after the date were averaged for each collection date to give a 9-day moving average of mean catch. The mean-trap catches were then plotted over time.

Because the data used were obtained from data collected as part of a large-scale test of control methods (Miller et al. 1984) and were calculated after that test was completed, temperature and rainfall records were obtained from a U.S. National Weather Service station about 10 Km east of the farms (Clarksville station). All weather data were transformed to metric equivalents. Rainfall was calculated as 3-day totals ending on the date of each fly count, and daily temperatures were expressed as the true mean-hourly temperature (TAVG), after adjustment for daylength and latitude (Bernhardt and Shepard 1978, Whalon and Smilowitz 1979, Waddill et al. 1976). A developmental threshold of 10°C was chosen because of observations from our colony (unpublished data).

Functions for the effects of temperature on face fly development, fecundity, mortality and activity were obtained from the literature (Turner and Hair 1966, Valiela 1969) and graphed (Fig. 1).

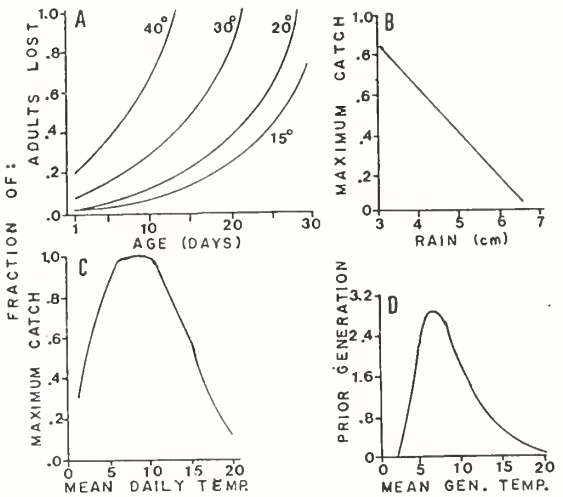

Fig. 1. Fractions of: A) adults lost (ALOSS); B and C) maximum possible catch due to rain (RACT) and air temperature (TACT) and; D) prior generation size (R_o).

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(1) $FD = (\sum_{o}^{n} TAVG-DT)/220$

Where FD is the fraction of development completed, n is days since eclosion of parents, TAVG is the mean hourly temperature and DT is the 10°C developmental threshold and 220 is the number of degree days above 10°C required to complete one generation (i.e., mean generation time equals 297 times TAVG to the -1.074 power),

(2) $\ln ALOSS = (-4.4228 + 0.0923 \times (TAVG-DT)) + 0.123 \times$ (adult age in days)

(3) $PSn = N_1 \times (1-ALOSS)$

Where the number of adults surviving at date n (PSn) is the fraction surviving to date (1-ALOSS) times the number of adults present at the start of the period (N1); and ALOSS is calculated for the age at the date of interest.

(4) $RACT = 1.551 + (-0.227 \times \sum_{n-3}^{n}$ Rainfall in cm)

Where n is the date of interest and RACT is bounded by 1 and 0.

(5) $TACT = 0.0121 + 0.2910T - 0.0246T^2 + 0.0005T^3$,

Where T is the mean average hourly temperature above 10°C (TAVG-DT). The fraction of maximum adult catch (AACT Fig. 1c) on any date is:

(6) $ACCT = TACT \times RACT$

(7) $\ln R_o = -8.6161 + 10.3034 \times \ln TMG + (-2.7371 \times (\ln TMG)^2)$,

Where R_o is the fractional change in numbers of flies between generations and TMG is the hourly temperature above 10°C for the entire generation period.

(8) $TMG = (\sum_{o}^{n} TAVG-DT)/n$

(9) $PCAT = PS_n \times ACCT$,

Where PCAT is the number of female flies caught in any 3-day period if a generation has not been completed (FD<1) and PSn is the number of available flies. If a generation is completed on the date of interest, then N_o is the number of flies in the prior generation and R_o is the fraction size of N_o in the new generation.

(10) $PCAT = (PSn + (NoxR_o)) \times ACCT$

if a generation is completed on the date of interest.

The maximum observed rate of increase in catch between generations on 40 farms over 6 years Md. was 3.0 , so R_o max was set at that value. The R_o term thus includes all immature and preovipositional losses at this locality, whether related to weather or not.

The R_o curve (R^2 = 0.99) was obtained from the data of Turner and Hair (1966) and assigned an upper limit of three. The RACT curve (R^2= 0.96) was derived from regression analysis of our field data for 1978, 1979 and 1980 and from recapture data of marked flies (Pickens et al. 1977). The adult fly temperature-activity curve (TACT) was derived by regression analysis from out daily mean temperatures and our daily catch data in 1978, 1979 and 1980 (R^2=0.99).

It was assumed that the three survey traps at each farm caught an insignificant fraction of the adult female population so that the number of survivors was not affected by prior catches (Pickens 1981).

The values of the constants in the formulae were calculated by conducting regression analyses of the calculated catches (based on curves derived from laboratory data) vs the actual fly catches in 1978, 1979 and 1980 until a best fit was obtained. Thus, although the shape of the curves is determined from laboratory studies, the determinate values are adjusted to fit observed field catches. The resulting model was tested by calculating expected catch values from the size and date of the first 9-day average catch (N_o) and from the weather data of 1981 and 1983 and then comparing a plot of those calculated catches with the 95% confidence intervals of the actual mean 3 trap, 3-day catches in those years (calculated by dividing each 3-trap, 9-day sum by 3 to get 3-trap mean catch for each 3 days). The size of the first adult population sampled in the spring (N_o) was determined by dividing the actual values for the first peak catch by the adult activity (ACCT) values for those dates.

Results and Discussion

The 9-day moving average catches of female face flies, calculated from 1981 and 1983 weather records, were within the limits on all of the averaged catches from three farms in 1981 (Fig. 2A) and were within the 95% confidence limits of all but three of the actual average 3 trap, 3-day, catches for a single farm in 1981 (Fig. 2B, June 29, July 6 and 9). The calculated catches were within the limits of all but one of the actual catches (Aug. 9) on a single farm in 1983 (Fig. 2C).

Since the 1981 and 1983 weather varied considerably from each other and from that in 1978, 1979 and 1980 (the years used to calculate constants), the fits obtained seem to indicate a fair approximation of expected catches when temperature and rainfall data are for the general area.

A critical point is the selection of the date and size of the first (overwintered) catch of flies in the spring. We recognize that this is only a very general model and may only be applicable to the catch and temperature values obtained under the conditions of our tests.

However, it does make it possible for us to make predictions about the effectiveness of any theoretical face fly control program by comparing actual catch values with the calculated expected catches adjusted for weather effects, and thus, avoid programs which are inefficient in either effectiveness or cost-benefit ratios. It also provides a means of determining whether the face fly population on a "check" farm is being reduced by unexpected factors.

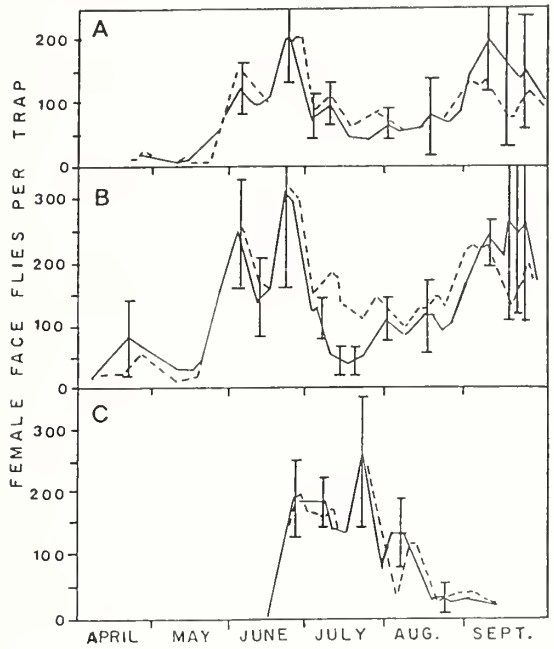

Fig. 2. Nine-day moving averages of actual (——) and calculated (----) catches of female face flies with 95% confidence limits indicated for some of the actual catches: A) averaged over three farms in 1981; B) on one dairy farm in 1981; C) on one beef cattle farm in 1983.

Acknowledgment

We particularly thank Mr. R. W. Thimijan, USDA-ARS, Agricultural Equipment Laboratory, for his help with the day-length and average hourly temperature computations.

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AGRICULTURAL COMPUTING: A REVIEW

S. M. Welch[1]

Introduction

In recent years it has become common to characterize our era as the "Age of Information." Not only is our technological understanding of the world around us proliferating, but, thanks to electronic technology, we have, in principle at least, access to more data affecting our daily activities than ever before. In practice, however, it is becoming increasingly difficult to manage this flood of information and to mold it into coherent decisions and policies.

While this problem affects many branches of society, it is becoming particularly acute in agriculture. This is leading to rapid adoption of computer technology both on the farm and among public agencies like the Extension Service which serve the farm community (10). Given the current pace of activity it is useful to review developments.

An Historical Perspective

The first uses of computers in agriculture occurred not long after the computer was first invented. These early applications tended to be fairly specific in nature like the 1958 computerization of milk production records for Dairy Herd Improvement Association (DHIA) members in Wisconsin. By the late 1960's, these individual applications had proliferated to the point that the concept of a centralized computer library had evolved. The concept of the extension computer delivery system was born when this library was coupled with interactive access through remote terminals which made computers available at farms and extension field offices. The two earliest such systems were TELPLAN in Michigan and the Computerized Management Network (CMN) funded by the Federal Extension Service at Virginia Polytechnic Institute and State University (11).

In terms of subject matter orientation, early delivery systems were dominated by agricultural economics and animal science topics although individual applications stemmed from a number of fields. The next conceptual step, however, emerged from the field of pest management. Pest management, of course, emphasizes the ideas of monitoring the status of pest and host populations, incorporating that data into the decision making process (which may involve computer models), taking appropriate control measures, and then remonitoring in an on-going fashion (8). With extensive data processing needs and, at that time, with centralized mainframes as the only available technology, the idea of a delivery system as a closed-loop, electronically linked, "on-line" system soon emerged (1).

This perspective resulted in greatly altered perceptions of the software content of delivery systems. Whereas, before, delivery systems had been collections of essentially self-contained applications, software in the on-line system was more specialized. Some programs for example, dealt only with entry and storage of scouting reports and other raw biological data. Other programs used that data to make recommendations and generate reports. There were specialized communication programs which handled electronic mail. The first such system, Michigan's Pest Management Executive (PMEX) System, also had a program called the SYSTEM MANAGER through which the user operated in a highly simplified error-tolerant environment with enhanced user friendliness (1).

In the latter half of the 1970's yet another technological leap forward occurred with the advent of "distributed processing". A major difficulty with the earlier mainframe centered approach was the high cost of communications to remote sites. In the PMEX system, for example, telephone charges exceeded computer expenses by a factor of 3 to 2. This made many applications like computer generated maps of pest distributions economically infeasible. The distributed approach circumvented this by placing smaller computers at area and/or county levels. Most tasks could, therefore, be dealt with locally with communication links only used for that minority of tasks requiring central mainframe resources. The first state to construct such a system was Indiana. This system has central computers located at Purdue with individual processors in each county (2). It was followed by other states including Kentucky, Florida, Texas, and California (10).

Recent Developments

This trend toward distributed systems accelerated rapidly in the early 1980's with the availability of microcomputers. These machines typically consist of a processor, main (or fast) memory, some form of auxiliary, magnetic disk memory, a printer, and a modem for telephone communications with larger, remote computers. Development of each of these components has been extremely rapid. For example, in the last 5 years the raw processing power of microprocessors has increased by a factor of 16, main and auxiliary memory capacities have enlarged 10 times, while cost for the most commonly purchased machines has remained constant in the range of $3-5,000 ($8,000 for the most powerful configurations).

This has completely altered the spectrum of uses to which computers are put in agriculture. Previously costs (even of remote timeshared systems) restricted applications to those for

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which no substitutes existed. Microcomputers, on the other hand, were viewed as an addition or replacement for several types of office equipment. This generated the concept of office automation where computers are used for (a) word processing, (b) spreadsheet (electronic ledgerbook) analysis, (c) filing (i.e. database) applications, (d) preparation of graphic materials, and (e) communication.

The result was the rapid spread of computer technology in state extension services. Prior to this, while many recognized the educational value of computer software, its use was something which has to be added to already overburdened annual workplans. Office automation, however, was an important productivity tool which could generate the efficiencies necessary to make new activities feasible. As a result, the majority of state extension services are at least performing limited experiments with microcomputers. One prediction is that 90 percent of all county offices will have microcomputers by 1990 (3).

The wide spread adoption of microcomputer technology and its incorporation into delivery systems is having significant impact on extension at the organizational and policy levels (10). Two of the most critical factors in the successful use of computers are planning and support for users. The former includes needs analysis and technology tracking while the latter deals with user training plus hardware and software troubleshooting. These requirements are forcing the evolution of state-level computer support staffs. Structurally, these support groups range from ad hoc committees to formalized administrative units. Their responsibilities may be limited to extension or include research and teaching elements as well.

An important regional support program is the North Central Computer Institute (NCCI). Located in Madison, Wisconsin, the NCCI is an association of the land grant institutions in the 12 north central states. It is funded jointed by those states and the W. K. Kellogg Foundation of Battle Creek, Michigan. Its overall objective is to support the agriculture and rural development computing efforts of its members in a variety of areas. These include facilitating multistate software and database developments and sharing, technical assistance, preparation of educational materials, staff development, etc. A similar institute has recently begun operations in the northeast (6, 8) and a consortium of western states has been proposed.

Significant policy issues have been generated by computers (5). These include, but are not limited to (a) delineation of appropriate agricultural computing roles for various groups of staff (researchers, instructors, agents, specialists, etc.), (b) administrative prioritization, approval, and resource allocation procedures for computer activities, (c) reward systems for staff involved with computer activities, (d) legal issues surrounding software development and distribution including copyrights, licensing arrangements, and cooperative agreements for multistate efforts, and (e) relations with the private sector. As might be expected, these are being resolved in a variety of fashions in different states.

The issue of private sector relations is particularly important because of the proliferation of agricultural computing business activities. These run the gamut from participation by computer industry majors like IBM and Control Data Corporation (either directly or through joint ventures) to small operations which may operate as a sideline to an existing agribusiness such as a private consultantship. Products may include hardware, software, access to information, or some combination of these. They may work in close cooperation with universities or (more commonly) independently. These efforts are expanding much more rapidly than public sector efforts, a trend that can be expected to continue. This is forcing a close consideration of issues like public sector competition with private enterprise, educational versus service roles in extension, the limits of consulting activities by public employees. etc.

Of course, all parties to these questions agree that the end product will be improvements in farm-level information management and decision making. In that vein, it is useful to look at on-farm applications of computers (4,9). There appear to be at least 3 generic areas. The first contains those farm office applications related to the business aspects of the enterprise. These can often be handled by the sorts of accounting packages, databases, and spreadsheet programs which are widely used in non-farm businesses. There are a number of these on the market including some that are specially packaged or adapted to particular agricultural operations. These can most easily be located through agricultural computing publications such as AgriComp or Farm Computer News.

The second category includes specific production decision making aids. While there are some examples of such software in use (e.g. feed ration programs) the need is much greater than the supply. One problem is that programs tend to be special purpose creations which only assist with selected pieces of the production process. In recent years the W. K. Kellogg Foundation has funded two projects which attempt to correct this. The first, in Florida, consists of a computerized reference guide dealing with all production aspects of several commodities. The second, in Kansas, provides a complete set of corn production decision aids and educational materials integrated with a field-by-field database and cost/return analysis module. Both systems have simplified user interfaces and make extensive use of computer graphics. The Florida program is currently being licensed for use in other states.

The final area of on-farm application is on-line monitoring and control. At present, there is more potential than practice in this area. The basic concept is the use of electronic sensors and microprocessors to acquire data, process it, and output control signals and/or management recommendations. Typical uses include irrigation scheduling, environmental control within farm structures, dispensing animal feed, fuel-efficient machinery operation, and pest control recommendations.

As on-farm use increases in the future so will the need for the communication of data to the farm. This will include weather information, commodity and market data, plus other general information of a diversified nature. At this time, a number of advanced communication technologies are under development or in service to meet these needs. Already in operation are a number of computer compatible information utilities such as CompuServe and the Source. They offer a wide range of services, mainly non-agricultural, and are accessible through dial-up electronic connections. There are also video oriented technologies like Line 21 systems and videotex. The former uses a normally invisible portion of broadcast television signals to encode frames of display information. They are extracted with a special decoder. In videotex systems the user electronically requests frames over the telephone. Coded information transmitted in response is used to generate graphic displays on the user's television or microcomputer. Radio is also being adapted for computer related uses. Recent FCC deregulation actions have made certain normally superfluous FM sidebands available for a variety of uses including data and software transmission. Until recently, they could be legally used only for remote paging services. At the same time, satellite receiver technology is becoming much less expensive. Services now exist which miltiplex inputs from various information providers and relay them by satellite to subscribers spread over large areas. All of these types of service can be expected to expand in the future.

Conclusion

At the present time all aspects of computer and communication technology are rapidly proliferating in agriculture. This provides many avenues for public agencies to enhance not only their educational and service roles, but also their internal operations as well. As with any new technique, there are, of course, concommitant policy and procedural issues and an ongoing need for planning and technology tracking. Institutional response to such complicated needs is, of course, not overnight. In the long run, however, we can expect these technologies to have the same magnitude of impact on agricultural practices farm mechanization has in decades past.

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FUTURE CONTRIBUTIONS OF MODELING TO LIVESTOCK AND MEDICAL HEALTH MANAGEMENT

Roger D. Moon[1/]

Introduction

The papers presented during the first day of this workshop illustrate the power of the modeling approach to biological research. A fair sampling of current efforts to model livestock and human host-parasite systems was presented during the status reports. The remaining intent of this workshop and the subject of this paper is to direct attention toward the future of modeling, both in research and in its applications. A view into the future of any activity must include some fantasy, wishful thinking, and with luck, a little prophesy. Just how much of each element is present in the following scenario will be left for future readers to judge.

People and Machines

During the next decade, more researchers will become familiar with the methods of systems analysis and simulation modeling. This trend will be fueled by students who receive greater training in mathematics, statistics and user level computer science. These researchers will be biologists first, using the modeler's tools to study and understand specific host-parasite life systems just as researchers now use microscopy, electrophoresis and chromatography.

Despite their growth in numbers, biological modelers will not function in isolation as many do today. Rather, more will cooperate with non-modeler counterparts in disciplines related by shared interest in a common animal or human health management problem. Communication among the disciplines will be facilitated by research models. However, not all members need be modelers. They need only understand the process of model building and be secure in their identities as essential members of the team.

For example, a small group whose purpose is to develop an optimum feedlot management policy might consist of an agricultural economist, an agricultural engineer, an animal scientist, an entomologist, a veterinarian and supporting staff. All will contribute their respective disciplines' expertise in defining and describing relationships among the relevant parts of the feedlot system. More importantly, the process of building the model will lead to more comprehensive questions, answers, and ultimately more robust management policies for feedlots.

The hardware and software used in modeling should continue to improve at a rapid pace. Mainframes, minicomputers, and microcomputers are becoming more powerful, especially in the case of the latter. Faster processors, larger memory chips and better data storage devices are being announced every quarter. Existing devices are becoming cheaper through mass production and market competition. Data acquisition and reporting systems will become more widespread, making market, weather and other data available to users on a real time basis.

Software interfaces between users and machines will become even more "friendly" than they are now. Standardization of operating systems will relieve users of the annoying need to learn a new system for each machine. Standardization will also facilitate the movement of data and code files among different machines. Reasonably standard high level programming languages such as PROLOG, FORTRAN, C, Pascal, and BASIC are now available and are being improved rapidly. These software developments will allow modelers to build, modify and move functioning blocks of code among machines and among different models. As a consequence, the biologist will be spared the technical details of using computers, and fewer wheels need be reinvented. In the future, it will be much easier to concentrate on biological and economic matters of greater interest.

Roles for Models

Models will contribute to the management of herd and human health systems in three major ways. First, as evident in the earlier papers, the process of specifying desired management goals and modeling the systems to be managed will force the organization of existing knowledge and make the "information gaps" obvious. In turn, developing models of the systems will be used to rank the importance of the gaps for subsequent research. Thus, the first set of major benefits from the modeling process will be to establish research priorities.

The second set of benefits will follow from improved understandings of the systems to be managed. Using the management criteria established for each system at the outset, simulation models will help researchers ask more focused questions, devise critical experiments and confirm through validation their understanding of how their systems function. Validated models can then be used to examine the biological and economic consequences of different management options. Optimization

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techniques will be used to identify the most desirable combination of options and levels of managerial input.

Technical breakthroughs in several areas may shape the future of livestock and medical pest management. New understandings of gene regulation and host immunology may make available new vaccines for protecting hosts from parasites and vectored pathogens. Notable examples include possible vaccines for falciparum malaria, trypanosomiasis and east coast fever. Developing knowledge about host responses to tick feeding may lead to methods for protecting individual cattle from acariasis. However, the expenses of using such methods may force development of a use policy based on complex logistical and economic considerations. Models of the host-parasite system will prove quite useful in formulating these use policies.

Models will also serve as vehicles for experiments which might be impossible or unwise to conduct in the field. For example, two options under current consideration for minimizing the development of pyrethroid resistance in horn fly involve conflicting strategies--the low dose and high dose strategies. Ignoring for the moment the difficulty of organizing and executing a critical, area wide field experiment with replication, an inappropriate strategy would actually cause the undesirable pyrethroid resistance to occur more quickly in nature. Clearly, certain experiments are too dangerous to be carried out in the real world and will best be conducted through simulation with realistic models.

A third major set of benefits concerns the timely use and dissemination of forecasts and predictions from the models to the ultimate users, i.e., herd and flock managers, health agencies and the military. Obviously, use of models in some production and protection systems will be more appropriate than in others, depending on the intensity with which the systems are managed, the number of viable actions available, and the risks and benefits to be derived.

The ultimate uses of research models will routinely be considered as the models are developed. Critical decisions about software design will be made early to avoid unnecessary recoding between the research and implementation phases. Software design will also encourage user feedback about the utility and performance of specific models. User response may have a large influence on product revisions that surely will occur as research and experience with specific managed systems accumulate.

Simple phenological models may be commonly used to schedule field activities such as sampling and applications of insecticides and drugs. Such models might reside on microcomputers and be driven from files of on-site weather data or coded directly into programmable field microprocessors requiring a minimum of the user's attention. More complex microcomputer based decision aids may assist managers in deciding whether or not treatments are economically justified at specific times. The programs would help conduct cost/benefit analyses using field sample data, expected yield losses and costs of labor and materials to control the pests.

In some cases, models might not be used directly by field personnel. Rather, direct use may be limited to technically trained specialists such as extension agents and health practitioners who in turn would communicate model predictions to their clientele. In the distant future, more complex biological models may ultimately be embedded in larger, more sophisticated management information systems, where a particular model would be invoked and run by other software, with the results being further processed and interpreted before being communicated to the ultimate user.

Concluding Thoughts

More than a half century has elapsed since simple analytical models were first used to understand the dynamics of malaria. The development of digital computers since 1945 has made it possible to analyze numerically complex host-parasite systems with much greater realism and in much greater detail. Today, biological modeling is an established discipline that contributes to most areas of biology, agriculture and medicine. This workshop provides every indication that modeling, if given adequate administrative support, will contribute substantially in shaping the future of medical and livestock health management.

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